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The background image on the cover is from the "tarpon scale wall" at the Tarpon Inn, Port Aransas Texas.

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# INTRODUCTION TO THE PROCEEDINGS OF THE FIRST INTERNATIONAL TARPON SYMPOSIUM

**G. Joan Holt and Scott A. Holt**

University of Texas at Austin, Marine Science Institute, 750 Channel View Drive, Port Aransas, Texas 78373

## Overview

Port Aransas, Texas, once the home of a world-class tarpon fishery that collapsed in the 1960's, was the site of the First International Tarpon Symposium on 15-16 February 2001. The symposium, organized by the scientists and anglers of Tarpon Tomorrow, was held on the campus of the University of Texas at Austin, Marine Science Institute. Tarpon Tomorrow is an organization of scientists and anglers dedicated to the research and restoration of tarpon and its habitat throughout its historical range.

Tarpon support valuable recreational fisheries in the Atlantic from North Carolina to Brazil and Africa, across the Gulf of Mexico and Caribbean Sea, and in the Pacific Ocean off Panama. In some parts of its range, notably in Florida, off Africa, and in much of the Caribbean, tarpon populations remain healthy. In other regions, the western Gulf of Mexico in particular, tarpon stocks have essentially disappeared. Though speculation abounds, the cause(s) for this decline are unknown. Researchers around the world have worked to increase our understanding of the ecology, life history, and population dynamics of this important sportfish. This knowledge is leading to an increased awareness of management opportunities which may arise to enhance existing populations and to re-establish tarpon in areas from where fisheries have been lost. Cooperation between researchers, fishery managers, government agencies and tarpon fishermen brings a spirit of optimism to the conservation and management of tarpon. This symposium was designed to foster this spirit. Researchers from the United States, Latin America, and Europe were invited to present their findings. Fishery managers had the opportunity to hear these reports and to discuss how this knowledge enhances management strategies. Information shared among the various interest groups at the symposium defined the current state of knowledge about tarpon and suggested direction for new and productive studies

## Symposium Structure

### Technical Sessions

Twenty oral presentations summarized results of tarpon research, monitoring, management, and related issues. Subjects included early life history, development, and

distribution of larvae; juvenile and adult ecology, including age and growth, migration, distribution, and population genetics; tarpon culture and enhancement; and tarpon fisheries regulations and management.

### Roundtable Discussions

Three roundtable discussions followed the technical sessions. The first discussion group examined the current status of tarpon research and future tarpon research opportunities and needs. Symposium speakers, representatives of granting agencies, and interested individuals discussed on-going research, needs for future research, and opportunities for financial support. Another roundtable discussion examined management of tarpon across the distribution of the species. Inter-agency and international cooperation was emphasized. The final roundtable discussion examined cooperation between fishermen, guides, scientists, and fishery managers. In particular, they explored ways fishermen and guides can assist in research and management, and ways scientists can provide relevant feedback to their collaborators.

## The Symposium Volume:

### Introduction

Mr. Ben Vaughn III, longtime coastal fisherman in the Port Aransas area and ardent supporter of fisheries conservations efforts along the coast, welcomed the symposium participants on behalf of the Marine Science Institute and the coastal fishing community. The following is a summary of those remarks.

"Way back, when…Some advantages of being older are that I have seen, hooked and caught more tarpon than most people have access to today. In Turtle Cove, the Port Aransas harbor, in the 50's and 60's we caught tarpon that were three or four feet long regularly in the shade of the boat houses; and in the early 50's, tarpon migrated by Port Aransas in great abundance…You could hear them coming, even see them coming for a mile. I've had as many as 50 big tarpon on in an afternoon. I don't know what's happened to them. There are any number of guesses, many made by scientists more knowledgeable than I am…the most logical explanation to me is that tarpon live a long time. The production of a mature tarpon, over its lifetime, may be no more than one or two tarpon, notwithstanding them laying millions of eggs, according to the scientists at the symposium. So, when you take one out of the reproductive milieu, you have struck a significant blow to the overall tarpon resource. Whether they were killed through pollution, the drying up of freshwater inflows, dynamiting for fertilizer, excess catches by recreational anglers, bycatch in nets—howsoever they were devastated—it means they are going to be a long time recovering…that is very concerning to those of us who have

both enjoyed seeing them and having the opportunity to fish for them. The loss of the resource is a tragedy, but scientific expertise should now be at sufficient levels to provide some answers, if we can raise sufficient money. Since tarpon are not very good to eat, like say, codfish, we haven't had the benefit of federal funding to gather reliable information about their migration or reproduction. It's obvious—to me at least—that the dearth of returns of tarpon tags using the dart tag, clip tag programs, are not going to give us information that's very helpful in deciphering the code of either tarpon migrations or reproduction. The "pop-up" tags that are monitored by satellite are very expensive, but it seems they would give us a better notion and a lot sooner rather than later...What the Tarpon Tomorrow organization is doing is providing a platform from which anglers and researchers can formally commence an effort to restore the population."—**Ben Vaughan III.**

## Organization

The first section in this volume includes peer-reviewed papers from six of the twenty oral presentations from the symposium. The first two papers by Blandon et al. and Garcia de Leon et al., discuss the population structure of tarpon from both a worldwide perspective and specifically for tarpon in the western Gulf of Mexico. Papers by Shenker et al. and Vega-Cendejas and Hernández provide information on recruitment and habitat utilization of larval and juvenile stages in Florida and the Caribbean. Guigand and Turingan describe morphology and feeding behavior of juvenile tarpon. The final paper by Winemiller and Dailey presents simulation models of population dynamics in tarpon. The next section presents abstracts of 12 presentations not developed into full papers covering a wide range of subjects and geographical settings. The final section provides a narrative of the three roundtable discussions.

## Acknowledgements

The symposium was organized under the guidance of the Tarpon Tomorow Planning Committee: Paul Swacina-Chair, Ivonne Blandon, Sam Caldwell, Joan Holt, Scott Holt, David McKee, Leo Trevino, Ben Vaughn, Bob Wallace, and Rocky Ward. It was sponsored by Coastal Bend Bays & Estuaries Program, Coastal Conservation Association of Texas, Texas A&M University-Corpus Christi Mariculture Program, Texas Parks and Wildlife and the University of Texas at Austin Marine Science Institute. Funding for publication of the proceedings was provided by Tarpon Tomorrow, Texas A&M University-Corpus Christi Mariculture Program and the Coastal Bend Bays & Estuaries Program. The organizers would like to thank the numerous reviewers whose work was essential in ensuring the quality of the full papers in this issue. We want to especially thank Venus Mills of the Marine Science Institute whose tireless efforts immeasurably improved both the symposium and this special volume.

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# STUDIES IN CONSERVATION GENETICS OF TARPON (*MEGALOPS ATLANTICUS*)
# I. VARIATION IN RESTRICTION LENGTH POLYMORPHISMS OF MITOCHONDRIAL DNA ACROSS THE DISTRIBUTION OF THE SPECIES

**Ivonne R. Blandon[1*], Rocky Ward[1], Francisco J. García de León[2], Andre M. Landry[3], Alfonso Zerbi[4], Miguel Figuerola[5], T. Cristina Gesteira[6], William Dailey[3], and Celene Acuña Leal[2]**

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## ABSTRACT

Tarpon, *Megalops atlanticus*, are among the elite game fishes of the world, supporting valuable recreational fisheries in the eastern Gulf of Mexico, the western Atlantic, and the Caribbean. However, the historically important Texas recreational tarpon fishery collapsed prior to the middle of the 20th century. In an effort to recover this resource, Texas Parks and Wildlife (TPW) has begun investigating additional management options including possible artificial culture and stocking of this species in Texas bays and estuaries. In order to establish enhancement guidelines to protect the genetic integrity of tarpon in the western Gulf of Mexico, a survey of genetic variation across the distribution of tarpon was undertaken. The present report details genetic analyses of the mitochondrial DNA (mtDNA) of 330 tarpon collected from 14 regions in the Gulf of Mexico, western Atlantic, eastern Atlantic, Caribbean, and Pacific of Panama. Restriction fragment length polymorphisms (RFLPs) of 4 mtDNA fragments amplified using the polymerase chain reaction (PCR) were analyzed. Extensive genetic variability was found with 57 composite haplotypes observed. Genetic differentiations among sites in the western Atlantic, and Caribbean were minimal, suggesting biologically significant gene flow among regions. Genetic differentiation in the Gulf of Mexico was detected, but did not appear to be geographically consistent. Sample size for African and Pacific collections was small and limited statistical power. African individuals were of the same composite haplotype observed most commonly across all regions of the primary distribution. Pacific tarpon were also less variable than those from other areas with

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composite haplotypes which were present but not common in the western Caribbean or elsewhere.

## INTRODUCTION

Tarpon range throughout coastal and nearshore waters of the Gulf of Mexico and Caribbean, and in the western Atlantic from the U.S. mid-Atlantic coast to Brazil (Hildebrand 1963; de Menezes and Paiva 1966). Peripheral populations occur off western Africa and along the Pacific coast of Central America. The Pacific population, founded by migrants across the Panama Canal (Hildebrand 1939), was thought to be non-reproductive (Swanson 1946; Wade 1962) but observation of numerous early juveniles in several rivers of western Panama (Charles Abernathy and Robert Stearns, personal communications) suggests the invasive tarpon are reproducing and perhaps expanding in range. In contrast, tarpon in the northwestern Gulf of Mexico are experiencing declines in population density (TPW unpublished data). In Texas, tarpon once supported a valuable recreational fishery with tournaments annually harvesting hundreds of reproductive-aged individuals and bringing significant income to local economies.

Tarpon are still caught off Texas but in numbers much reduced from a few decades ago. In an effort to reverse this decline, TPW instituted catch-and-release regulations in 1991, with limited retention of trophy-class individuals (80 inches or greater total length) through use of a special trophy-tag. Despite these regulatory changes, the Texas tarpon fishery is not considered recovered and captures remain a fraction of historical landings. In 1998, TPW instituted a 'tarpon initiative' with the goal of applying innovative management options to reestablish the valuable tarpon fishery in Texas waters.

One aspect of this initiative sought to artificially enhance the tarpon population resident in Texas waters by developing protocols for spawning and culturing tarpon at TPW's salt-water hatcheries. The goal of this work was to release juvenile tarpon into Texas bays and estuaries to supplement naturally-spawned cohorts. By policy, a thorough investigation of stock structure is conducted prior to stocking artificially-cultured organisms into marine waters by the Coastal Fisheries Division of TPW. This precaution is designed to protect the genetic integrity of enhanced populations, conserving both within-region variation and between-region differences in genetic characteristics.

Genetic variation in tarpon has been described in only one report to date. McMillan-Jackson et al. (1993) utilized allozyme electrophoresis, restriction fragment length polymorphism (RFLP) analysis of mitochrondrial DNA (mtDNA), and morphological variability to compare tarpon from the eastern Gulf of Mexico, Caribbean, western Atlantic, and off western Africa. Samples from all areas, except Africa, appeared to be members of a single population. Genetic variability within this population was extensive;

however, differences between sites were not pronounced, and gene flow was estimated to be high. African sample sizes were small and characterized by unique alleles for allozyme markers and fixation for RFLP patterns in mtDNA not common elsewhere, suggesting tarpon from African waters were genetically isolated.

The study by McMillan-Jackson and her colleagues, by not including samples from the Gulf west of Florida, left unanswered questions about the relationship of tarpon from the northwestern Gulf to conspecifics in the eastern and southern Gulf and across the remainder of the species' distribution. These questions must be answered to ensure that sources of broodfish, larvae, and/or eggs used for experiment or stocking do not compromise the genetic resources of this species in the western Gulf of Mexico. Design of the proposed stocking program will benefit from estimates of genetic variability in the natural population allowing determination of the minimum number of broodfish contributing to a stocking cohort needed to avoid negative impacts (Allendorf and Ryman 1987). Other aspects of tarpon fishery management may benefit from an understanding of stock structure. For example, if Mexico and Texas share a tarpon stock, the recovery of the Texas tarpon fishery may require cooperation with federal, state, and private conservation agencies in Mexico. The objectives of this study were to obtain information on within- and among-region genetic variability of tarpon, with the goal of providing a description of stock structure of this species necessary for scientific management and to provide input into enhancement strategies. This report describes a study utilizing molecular techniques to explore variability in the mitochondrial genome of tarpon. Mitochondrial DNA (mtDNA) offers a unique perspective on the genetic diversity and differentiation inherent in natural populations (Avise 1987). This maternally inherited molecule has been shown to evolve rapidly in many animals (Neigel 1994), exceeding rates of change for single-copy nuclear genes by a factor of about 10 (Brown et al. 1979). It has proven to be a rich source of information on closely related populations (Moritz et al. 1987; Ferris and Berg 1988; Ovenden 1990).

## METHODS

The general strategy followed in this study was that of Chow et al. (1993) in which targeted regions of the mtDNA genome were PCR amplified (Saiki et al. 1988) using conserved primers (Kocher et al. 1989), then digested with restriction endonucleases to produce fragments whose number and size depended upon the presence or absence of recognition sites.

PCR allows analysis of small amounts of tissue collected by minimally invasive techniques (Whitmore et al. 1992) a characteristic especially important in tarpon, which are often accessed during recreational captures requiring minimal handling and release of fish. Samples were primarily scales obtained from a variety of sources (Figure 1). Most

Texas samples were obtained by TPW personnel during routine resource sampling or opportunistically following fish kills. Recreational fishermen and guides from across the distribution of the species were enlisted to collect scales from catch-and-release captures. Several samples were obtained from tournaments in Mexico, Texas, Louisiana, and Florida and from fish markets in Mexico and Puerto Rico. Scales were placed in 100% ethanol (diluted to 70% with DI water), refrigerated for 24 hours, and then stored at room temperature until shipment to the Perry R. Bass Marine Fisheries Research Station.

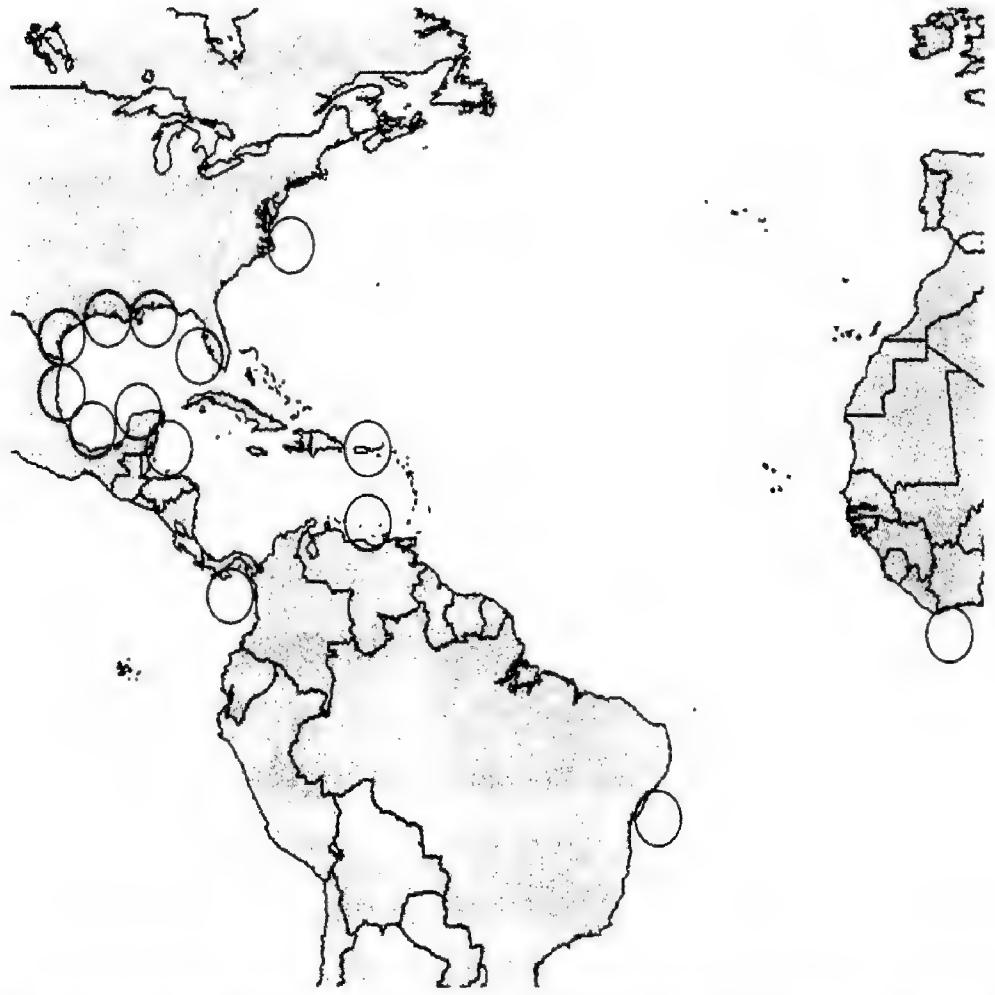

Figure 1. Sampling sites and areas for tarpon (*Megalops atlanticus*) included in present study. Localities are described in text

Genomic DNA was recovered from scales using the Puregene DNA isolation kit (Gentra Systems, Minneapolis, MN). Four mtDNA fragments were PCR amplified using primers designed for broad application among teleost fishes (Table 1). Reactions were set employing Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Piscataway, NJ) in 25 µl reactions containing 1.0 µl of template DNA and 1.0 µl of each member of the primer pair. Amplifications were performed using the Techne Genius thermalcycler (Techne Inc., Princeton, NJ) programmed for the following profile: 35 cycles at 95 °C (60 s), 48 °C (75 s), 72 °C (90 s), followed by 72 °C for 7 min, then a 4 °C hold.

Table 1. Primer pairs used to amplify mtDNA fragments in tarpon.

| Fragment | Sequence (5'-3') | Fragment length[1] | Reference |
|---|---|---|---|
| Cyt *B* | ATGATGACCGCCTTCGTAGGCTA | 1300 | Canatore 1994 |
| | AATTGTGTGACTGGTCGGAATGT | | |
| ND 2 | CCGGATCACTTTGATAGAGT | 1600 | King[2] |
| | CGCGTTTAGCTGTTAACTAA | | |
| ND 4 | CAAGACCCTTGATTTCGGCTCA | 1900 | Bielawski and Gold 1996 |
| | CAAGAGTTTCAGGCTCCTAAGACCA | | |
| 12S/16S rRNA | AAAAAGCTTCAAACTGGGATTAG | 1900 | King[2] |
| | CCGGTCTGAACTCAGATCACGT | | |

[1]Estimated by comparison with molecular weight standards.
[2]Primer pair sequences provided by T. L. King.

A sub-set of amplification products were digested with 26 restriction endonucleases: *AciI, AluI, BfaI, BsaJI, BslI, BsoFI, BstUI, Cac8I, DdeI, Fnu4HI, HaeIII, HhaI, HinfI, MaeIII, MboI, MnlI, MseI, MspI, MwoI, NlaIII, NlaIV, RsaI, Sau96I, ScrFI, TaqI*, and *Tsp509I*. Digestion protocols provided by restriction enzyme supplier were followed. Results were screened for polymorphism and quality of digest. Polymorphic RFLP patterns were confirmed through repeat digestions separated on 2% agarose gels. Fragment sizes were determined by comparison with pGEM molecular weight DNA markers (Promega Corporation, Madison, WI) and analyzed using the Gene Profiler 1-D Gel Analysis and Databasing Program (Scanalytics, Inc., Fairfax, VA).

Nucleotide sequence divergence among sampling sites was estimated using the software package REAP (McElroy et al. 1992). Phylogeographic relationships of composite haplotypes were examined using minimum-length parsimony networks. Composite haplotypes were connected based on similarity of inferred restriction site sequences. Changes in restriction site sequence were assumed to reflect single nucleotide gain, loss, or point mutation.

Analysis of molecular variance (AMOVA; Excoffier et al. 1992) was performed on the genetic analysis software package ARLEQUIN (Schneider et al. 1999) to test

homogeneity of mtDNA haplotype distributions across sample sites. Estimates of genetic variance components and Φ-statistics (hierarchical *F*-statistics equivalents) were generated along with statistical significance by random permutation (1,000 replicates) for all collection sites except Africa and Panama Pacific which were precluded from analysis due to small sample sizes. A separate hierarchical comparison was conducted for Gulf of Mexico localities. $F_{ST}$ values calculated by ARLEQUIN were used to estimate the annual number of migrants ($M$) between sampling sites. ARLEQUIN was also used to test the hypothesis that composite haplotypes were randomly distributed among sampling sites. Exact tests were applied as described by Raymond and Rousset (1995) including error estimation of $P$ values associated with the contingency table. Significance levels for multiple tests carried out simultaneously were adjusted using the sequential Bonferroni method (Rice 1989).

## RESULTS

Nine PCR product/restriction enzyme combinations produced informative patterns (Table 2). The cyt *b* fragment yielded polymorphic patterns when digested with *AluI*. Polymorphic patterns were obtained when ND-2 was digested with *DpnII, HaeIII*, and *NlaIII*. The ND-4 fragment yielded polymorphic patterns after digestion with *TaqI, NlaIII*, and *DpnII*. The 12S/16S fragment digested with *AluI* and *Sau96I,* was also found to be informative. From these patterns, 57 composite haplotypes were identified.

Table 2. Spatial distribution of composite mtDNA haplotypes of tarpon (*Megalops atlanticus*). Letters are digestion patterns for *AluI* of cyt *b*, *NlaIII, HaeIII,* and *DpnII* digests of ND-2, *NlaIII, TaqI,* and *DpnII* digests of ND-4, and *Sau96I* and *AluI* digests of 12S-16S PCR products. Sample codes: NC=North Carolina, PR=Puerto Rico, BR=Brazil, VZ=Venezuela, WC=western Caribbean, ML=lower Mexico, MM=middle Mexico, MU=upper Mexico, TL=lower Texas, TU=upper Texas, LA=Louisiana, and FL=Florida.

| Hapl No. | Comp. Hapl. | Samples | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NC | PR | BR | VZ | WC | ML | MM | MU | TL | TU | LA | FL |
| 1 | AAAAAAAAA | 12 | 6 | 4 | 2 | 11 | 8 | 25 | 10 | 9 | 12 | 18 | 21 |
| 2 | AAAACAAAA | - | - | - | - | - | - | 1 | - | - | - | 2 | 1 |
| 3 | AABAAAAAB | - | - | - | - | - | - | 1 | 1 | - | - | - | 1 |
| 4 | ABAAAAAAA | - | - | - | - | 1 | 1 | - | - | - | - | - | 2 |
| 5 | AAAABAAAA | 2 | 2 | 1 | - | 6 | 4 | 4 | 3 | - | 6 | - | 4 |
| 6 | AAAAAAAAB | 1 | 1 | - | - | 2 | 1 | 4 | - | 2 | - | 1 | 3 |
| 7 | BAAAAAAAA | 2 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 |
| 8 | AACDAAAAB | - | - | - | - | 1 | - | 1 | - | - | - | - | - |
| 9 | CAAABAAAA | - | - | 1 | - | - | - | 1 | - | - | - | 2 | - |

Table 2. Continued

| Hapl No. | Comp. Hapl. | Samples | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NC | PR | BR | VZ | WC | ML | MM | MU | TL | TU | LA | FL |
| 10 | AAAAAAABB | - | 1 | - | - | - | 2 | - | - | - | 1 | - | 3 |
| 11 | CAAABBAAA | - | - | - | - | - | - | - | - | - | - | - | - |
| 12 | AAAAAAABA | - | 1 | 2 | - | - | 2 | 3 | 1 | - | 1 | 3 | 4 |
| 13 | AAAADAABA | - | - | - | - | - | - | 1 | - | - | - | - | - |
| 14 | AAACBACAA | - | - | - | - | - | - | - | 1 | - | - | - | - |
| 15 | CAAAAAAAB | - | - | - | - | - | - | - | 1 | - | - | - | - |
| 16 | AAAAAACAA | - | 1 | - | - | - | - | - | 1 | - | - | - | - |
| 17 | CAAAAAAAA | - | - | - | - | 1 | 1 | - | 1 | - | 1 | 2 | 2 |
| 18 | AAABAAAAA | - | - | - | 2 | 1 | - | - | 3 | - | 1 | - | - |
| 19 | AAAADAAAA | 1 | - | - | - | - | - | - | 1 | - | - | - | - |
| 20 | AAAAABAAA | - | - | - | - | 1 | - | - | 2 | - | 1 | 1 | - |
| 21 | CAAAAAABA | - | - | 1 | - | - | 1 | - | - | - | - | - | - |
| 22 | AAABBAAAA | - | 1 | - | - | - | 1 | - | - | 3 | - | - | - |
| 23 | AAAABAAAB | - | - | - | - | 1 | - | - | - | - | 2 | - | 1 |
| 24 | BAAAAAABA | - | - | - | - | - | 1 | - | - | - | - | - | - |
| 25 | AABAAAAAA | - | - | - | - | 2 | - | 2 | - | - | - | - | - |
| 26 | AAAABAABA | - | - | 1 | - | - | - | 1 | - | 1 | 1 | 1 | 2 |
| 27 | ABAABAAAA | - | - | - | - | 1 | - | - | - | - | - | - | - |
| 28 | AAAABAACB | - | - | - | - | 1 | - | - | - | - | - | - | - |
| 29 | AAAABBABA | - | - | - | - | 1 | - | - | - | - | - | - | - |
| 30 | AAAAAADAA | - | - | - | - | 1 | - | - | - | - | - | - | 1 |
| 31 | AAAAAABAA | - | 1 | - | - | - | - | - | - | 2 | - | - | 1 |
| 32 | ABBAAAAAA | - | - | - | - | - | - | - | - | 1 | - | - | - |
| 33 | AAABAAAAC | - | - | - | - | - | - | - | - | 1 | - | - | - |
| 34 | AAABACAAA | - | - | - | - | - | - | - | - | 1 | - | - | - |
| 35 | AAAACBAAA | - | - | - | - | - | - | - | - | 1 | - | - | - |
| 36 | BABABAAAA | - | - | - | - | - | - | - | - | - | 1 | - | - |
| 37 | AAADCAABA | - | - | - | - | - | - | - | - | - | 1 | - | - |
| 38 | AABABAAAA | - | - | - | - | - | - | - | - | 1 | 1 | - | - |
| 39 | AAAABBAAA | - | - | - | - | - | - | - | - | 1 | - | - | - |
| 40 | BAAABAAAA | - | - | - | - | - | - | - | - | - | 2 | - | 1 |
| 41 | ACAAAAAAB | - | - | - | - | - | - | - | - | - | - | - | - |
| 42 | AAAABCAAB | - | 1 | - | - | - | - | - | - | - | - | - | - |
| 43 | CAAABAABB | - | 1 | - | - | - | - | - | - | - | - | - | - |
| 44 | AAAABAABB | - | 1 | - | - | - | - | - | - | - | - | - | - |
| 45 | AAABDAAAA | - | 1 | - | - | - | - | - | - | - | - | - | - |
| 46 | CAABAAAAB | 1 | - | - | - | - | - | - | - | - | - | - | - |
| 47 | BAAAAACAA | 1 | - | - | - | - | - | - | - | - | - | - | - |

Table 2. Continued

| Hapl No. | Comp. Hapl. | Samples | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NC | PR | BR | VZ | WC | ML | MM | MU | TL | TU | LA | FL |
| 48 | CABBAAAAA | 1 | - | - | - | - | - | - | - | - | - | - | - |
| 49 | AAADAAAAA | 1 | - | - | - | - | - | - | - | - | - | - | - |
| 50 | AAACBAAAA | 1 | - | - | - | - | - | - | - | - | - | - | - |
| 51 | AAAABABAA | - | - | - | - | - | - | - | - | - | - | 1 | - |
| 52 | ACAAAAAAA | - | - | - | - | - | - | - | 1 | - | - | 1 | - |
| 53 | ABAAAAABB | - | - | - | - | - | 1 | - | - | - | - | - | - |
| 54 | ABCAAACAA | - | - | - | - | - | - | - | - | 1 | - | - | - |
| 55 | CAAABABBA | - | - | - | - | - | - | - | - | 1 | - | - | - |
| 56 | AAAABAACA | - | - | - | - | - | - | - | - | - | - | 1 | - |
| 57 | AABAAAABA | 1 | - | - | - | - | - | - | - | - | - | - | - |

Haplotype 1 accounted for 43.2% of individuals surveyed and was the most common haplotype in every population except Panama Pacific. The next most common composite haplotype (haplotype 5) accounted for 9.9%. Thirty composite haplotypes were observed in single individuals. Every haplotype represented by more than one individual occurred in at least 2 sites.

The number of composite haplotypes per sample site ranged from 1 in Africa to 15 in Florida and corresponds closely to the number of individuals included in each sample (Table 3). Intrapopulational nucleotide sequence diversities ranged from 0.681 (middle coast of the Mexican Gulf) to 0.895 (Puerto Rico) with an overall nucleotide sequence diversity of 0.809.

Minimum-length parsimony networks (Figure 2) revealed that each observed composite haplotype could be derived from the most common haplotype (haplotype 1) by a minimum of 4 restriction site changes. The 4 most common composite haplotypes each formed 'hubs' (in the sense of Gold and Richardson 1998a) about which related haplotypes grouped. Most hub groupings were spread broadly across the sampled distribution of tarpon. Two small groups, hubs 20 and 25, were restricted to the Gulf of Mexico and western Caribbean. The occurrences of these groups of haplotypes were low (N=6 and N=5, respectively) and they may well have been present but missed in Atlantic samples. In the Gulf of Mexico, Hub groups 10 and 25 were absent from eastern sampling sites, but were not ubiquitous in the western Gulf. No obvious clines in hub frequency were observed in the Gulf of Mexico, except for hub 6 which displayed a gradual reduction in frequency from lower Mexico (17.39%) to Louisiana (2.94%), the frequency of this hub group recovered to 14.58 in Florida tarpon.

Table 3. Intrapopulational nucleotide sequence diversities based on mtDNA haplotypes among samples of tarpon (*Megalops atlanticus*). Codes for sampling sites are given in Table 1, except AF=Africa and PA=Pacific of Panama.

| Sample | No. Individuals | No. Haplotypes | Nucleotide sequence diversity (±SD) | Haplotype diversity (±SD) |
|---|---|---|---|---|
| NC | 24 | 11 | 0.754 ± 0.093 | 0.068±0.045 |
| PR | 18 | 12 | 0.895 ± 0.065 | 0.077±0.050 |
| BR | 10 | 6 | 0.844 ± 0.103 | 0.048±0.037 |
| VZ | 5 | 3 | 0.800 ± 0.164 | 0.036±0.033 |
| WC | 31 | 14 | 0.845 ± 0.053 | 0.066±0.043 |
| ML | 23 | 11 | 0.858 ± 0.058 | 0.057±0.039 |
| MM | 45 | 12 | 0.681 ± 0.075 | 0.048±0.034 |
| MU | 27 | 13 | 0.852 ± 0.060 | 0.060±0.040 |
| TL | 25 | 13 | 0.863 ± 0.060 | 0.100±0.061 |
| TU | 31 | 13 | 0.821 ± 0.058 | 0.064±0.042 |
| LA | 33 | 11 | 0.699 ± 0.086 | 0.040±0.030 |
| FL | 48 | 15 | 0.795 ± 0.056 | 0.051±0.035 |
| AF | 2 | 1 | * | * |
| PA | 3 | 3 | * | * |
| Total | 325 | 57 | 0.809 ± <0.001 | 0.060±<0.001 |

* Diversity values not calculated for samples with <5 individuals.

Statistically significant comparisons were found with Analysis of Molecular Variance (AMOVA) both within the Gulf of Mexico and among all sampling sites (Table 4), with $\Phi$ values of 0.017 ($P < 0.01$) for the Gulf sites and 0.017 ($P < 0.01$) among all collections. Overall, examinations of variance in haplotype distribution suggest differences across the Gulf of Mexico, across the sampled distribution of the species, and perhaps between some regions may have been present. However, differentiation was not great across the sampled distribution of tarpon, as attested by the $\Phi$-statistic of 0.017 and elevated estimates of migration (Table 5). Estimates of the number of migrants per generation ranged from 2 between Brazil and Venezuela to infinity for 15 of the 72 comparisons. The gene flow resulting from this level of migration may have acted to

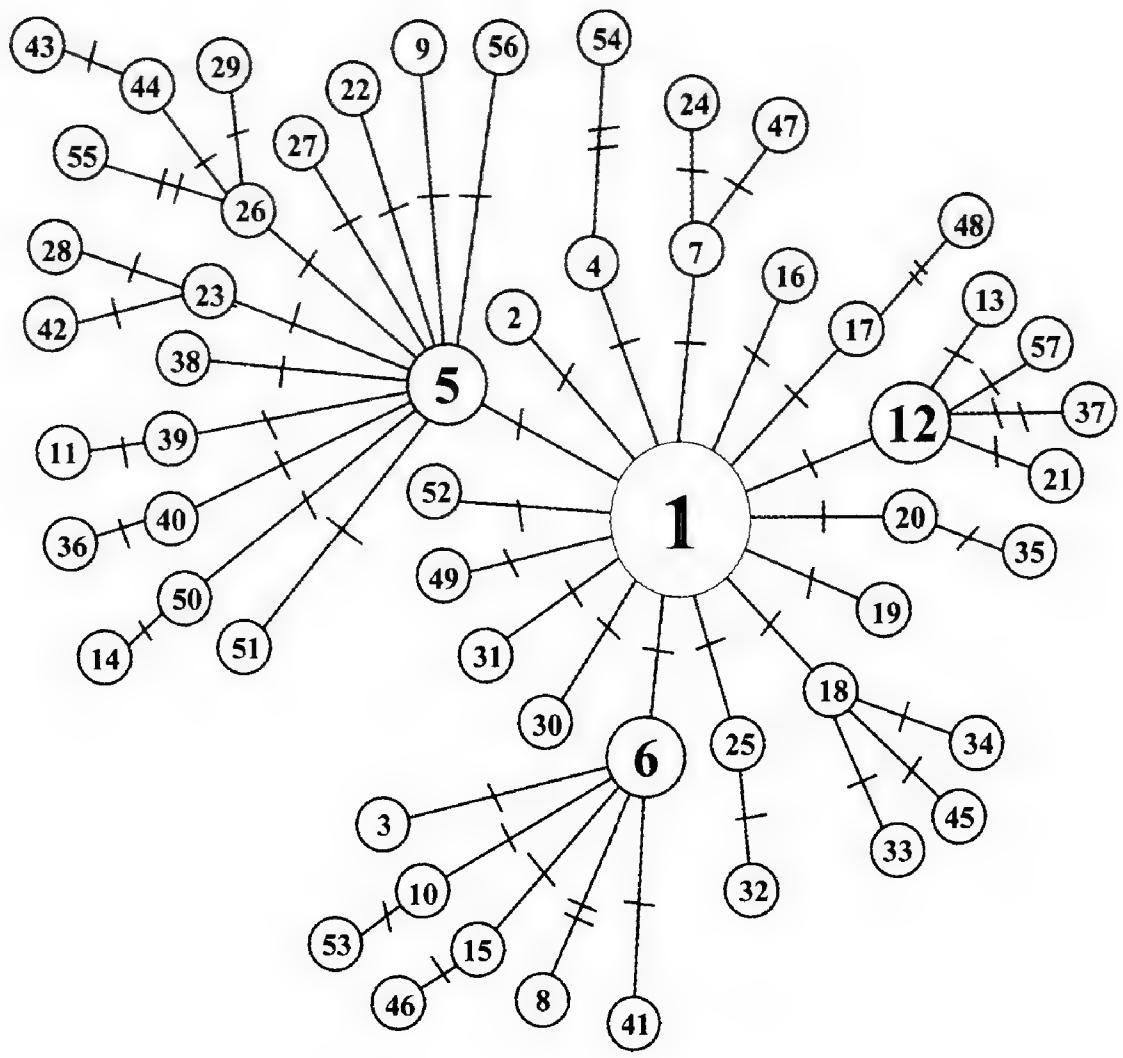


Figure 2. Minimum-length parsimony network of mtDNA composite haplotypes in tarpon (*Megalops atlanticus*). Numbers refer to composite haplotypes listed in Table 1. Number of hash marks is proportional to the number of inferred restriction site changes. Size of circle indicates observed frequency of that composite haplotype; large circle N=138, medium circles N=15-32, small circles N<15.

Table 4. Analysis of molecular variance (AMOVA) among mtDNA haplotypes of tarpon.

| Variance component | Observed partition | | Φ Value | *P*[a] |
|---|---|---|---|---|
| | Variance | % Total | | |
| All samples[b] | | | | |
| Among samples | 0.01408 | 1.66 | 0.017 | 0.008 |
| Within samples | 0.83660 | 98.34 | | |
| Gulf samples | | | | |
| Among samples | 0.01409 | 1.72 | 0.017 | 0.007 |
| Within samples | 0.80671 | 98.28 | | |

reduce population differentiation across the distribution of this species (Table 5). Of the 72 pair-wise comparisons 59 were shown by exact tests to be similar, though no comparison reached statistical significance after the Bonferroni correction was applied. Among those comparisons approaching significance, geographic proximity was often not a factor. Five of the 12 sampling sites were genetically similar to at least one neighboring site and 3 collection locales, Mexico-upper, Texas-lower, and Texas-upper sites, approached statistical significance when compared with both neighboring sites. This failure to find geographic cohesion in patterns of genetic variability across the sampled distribution of tarpon is reflected in the neighbor-joining topology generated from the matrix of interpopulation divergence values (Figure 3).

Table 5. Above the diagonal, Estimates of migrants per generation for tarpon (*Megalops atlanticus*). Below the diagonal, exact test for pair-wise population differentiation for tarpon (*Megalops atlanticus*). Values that approach statistical significance are shown, as is the estimation of error for those values. Codes for sampling sites are given in Table 1.

| | NC | PR | BR | VZ | WC | ML | MM | MU | TL | TU | LA | FL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NC | | 14 | 9 | ∞ | ∞ | 18 | ∞ | ∞ | 329 | 50 | 44 | 29 |
| PR | | | 51 | 6 | 243 | ∞ | 11 | 17 | ∞ | 200 | 7 | 32 |
| BR | | | | 2 | 11 | ∞ | 8 | 9 | 13 | 22 | 19 | 16 |
| VZ | | | | | 6 | 5 | 6 | ∞ | ∞ | 5 | 5 | 5 |
| WC | | | | | | 27 | 465 | ∞ | ∞ | ∞ | 13 | 50 |
| ML | | | | | | | 26 | 17 | 18 | 21 | 30 | ∞ |
| MM | | 0.085 ±0.008 | | | | | | 849 | 19 | 20 | 51 | ∞ |
| MU | | | | | | | 0.042 ±0.012 | | ∞ | 28 | 108 | 27 |
| TL | 0.080 ±0.017 | | | 0.001 ±0.002 | 0.027 ±0.009 | 0.002 ±0.003 | 0.005 ±0.005 | | | 43 | 10 | 17 |
| TU | | | | | | 0.023 ±0.009 | | 0.003 ±0.003 | | | 9 | 14 |
| LA | | 0.018 ±0.009 | | 0.001 ±0.001 | 0.024 ±0.010 | | | 0.008 ±0.007 | 0.023 ±0.008 | | | 52 |
| FL | | | | | | | | 0.010 ±0.008 | | | | |

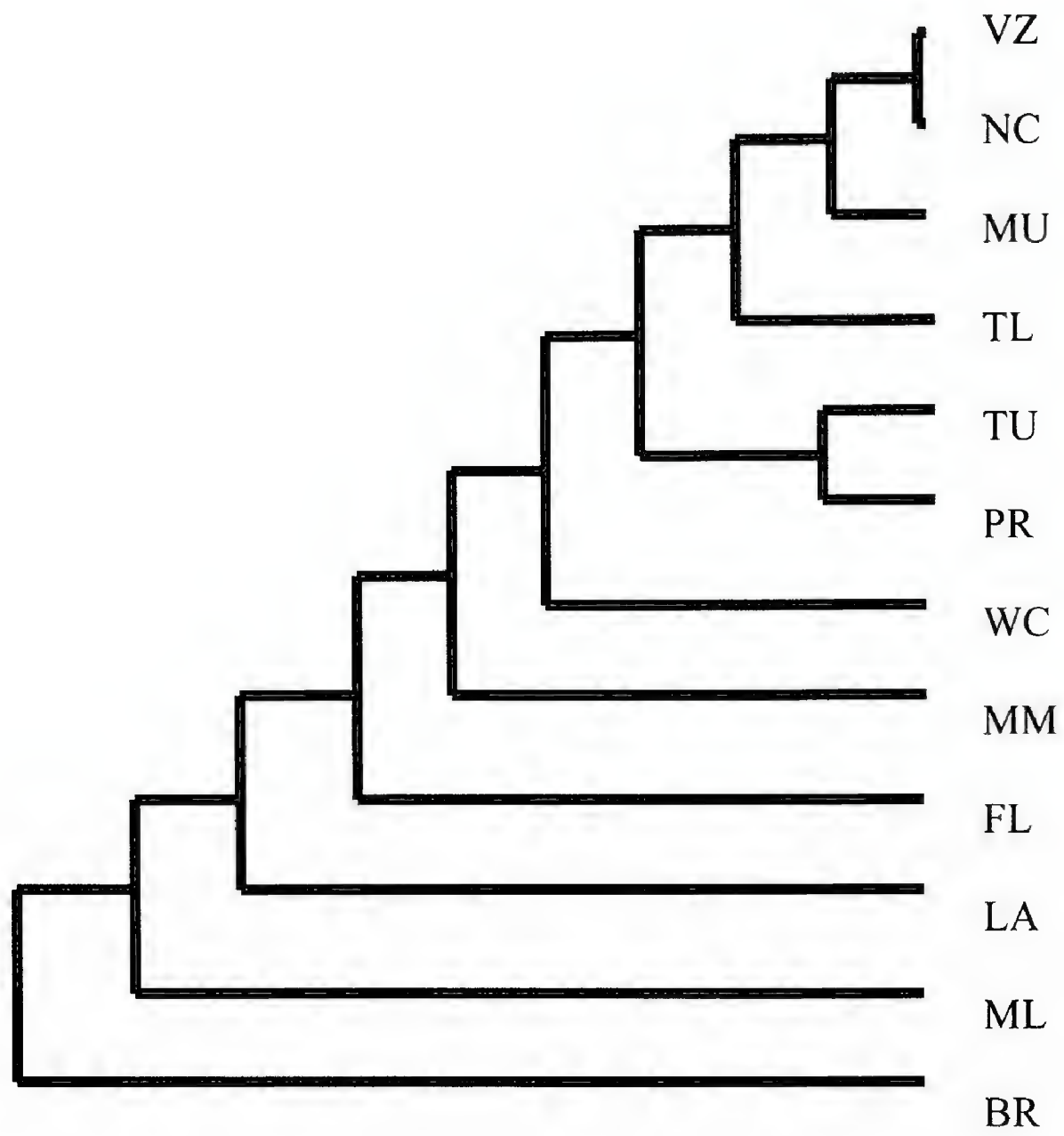


Figure 3. Neighbor-joining topology generated from matrix of interpopulational mtDNA nucleotide sequence divergence values among samples of tarpon (*Megalops atlanticus*). Codes for sampling sites are given in Table 1.

Collection sites off Africa and the Pacific coast of Panama were not included in these analyses due to small sample sizes (N=2 for Africa and N=3 for the Pacific). Examinations of these collections, however, allow some observations to be made. Both African individuals possessed the same composite haplotype, the same haplotype that was most common in the 12 sample localities included in the analysis. Two of the 3 individuals from the Pacific of Panama were found to have haplotype 6 and the third had haplotype 23. Neither composite haplotype was among the 3 most common haplotypes observed across the sampled distribution of this species; however, both were observed in western Caribbean tarpon.

## DISCUSSION

Analyses of mtDNA variation in tarpon demonstrate a genetically diverse species that is not, over most of its distribution, genetically differentiated into distinct stocks. This condition is not uncommon among marine organisms, where large effective population sizes, highly mobile adults, extensive dispersion of eggs and larvae, and/or lack of barriers to gene flow may operate to reduce genetic subdivision (e.g., Bowen and Avise 1990; Arnason et al. 1992). Life history and biogeographic factors may act to constrain gene flow, allowing spatial structuring to occur (Avise et al. 1987; Crosetti et al. 1994; Graves and McDowell 1995). Gene flow in tarpon appears to be so extensive in the western Atlantic and Caribbean as to prevent the accumulation of genetic differences in these regions. These results are similar to the earlier findings of McMillan-Jackson et al. (1993) with extensive within-sample genetic variation, limited population subdivision, and elevated estimates of gene flow consistent with the known life history of tarpon.

Evidence of genetic differentiation within the Gulf of Mexico was obtained using AMOVA which found significant differences among sample variability. These findings were supported by observed changes in haplotype frequency in the western Gulf of Mexico. Despite this apparent departure from genetic heterogeneity, there are no abrupt breaks in haplotype frequency, no obvious clines in haplotype frequency or diversity indices across the Gulf of Mexico, nor are cluster analyses able to identify distinctive groupings of Gulf of Mexico collections.

The peripheral tarpon populations included in this study, off Africa and the Pacific coast of Panama, do appear to be genetically isolated from other demes. Small sample size limits statistical power, however the 2 individuals composing the African sample possessed the same composite haplotype. This finding is similar to the genetically depauperate African tarpon examined by McMillan-Jackson et al. (1993) except that, unlike the earlier survey, which found African fish to be genetically distinct from western Atlantic samples, the current study found African tarpon to have the same composite haplotype that was most common across the contiguous distribution of the species. Tarpon from the Panamanian Pacific also appear to have reduced genetic diversity. This sample, in contrast with African tarpon, has haplotypes that, while occurring in the western Caribbean (the probable source for the Pacific population), are not among the most common observed in that region. Additional studies may show Pacific tarpon to be genetically divergent due to founder effect, a hypothesis that may be tested once a larger sample is obtained.

Absence of spatial structuring across the primary distribution of tarpon has important management implications. Presence of a single undifferentiated population in the Gulf of Mexico means failures of local Gulf tarpon fisheries, such as occurred in Texas, may be attributable to events and processes occurring elsewhere. Texas is located near the

physiological limits imposed by low temperature on tarpon (Zale and Merrifield 1989 and citations therein), especially during harsh winters, and may be dependent upon seasonal migration of adults from other regions of the Gulf to sustain its fishery. Mexico is the most likely source of Texas tarpon and anecdotal evidence reports tarpon in Mexican waters are presently in decline (Mario Cruz Ayala, personal communication). This suggests the collapse of the Texas fishery may be due to loss of habitat or overfishing in Mexico, and strongly implies that recovery of the Texas tarpon fishery requires cooperative efforts between Texas and Mexican management agencies.

These results have important implications for proposed enhancement efforts. First, geographically consistent differences were not found across the Gulf of Mexico, suggesting procurement of tarpon eggs, larvae, and/or broodfish may be made from sites outside of Texas without compromising the genetic integrity of Texas tarpon. It should be borne in mind, however, that future analyses based on different genetic markers may reach different conclusions (see the research on *Sciaenops ocellatus* population genetics; Gold et al. 1993; Gold and Richardson 1994, 1998b; Gold et al. 1999), and it may be prudent to obtain tarpon for enhancement from sites as near to Texas as possible. The second major point concerns the extensive variability observed in tarpon. Broodfish numbers should be great enough to insure that the genetic variability of the stocked cohort approximates that of naturally occurring tarpon. Failure to address this concern could result in release of large numbers of genetically depauperate fingerlings that might, should they survive, negatively impact the enhanced population.

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# STUDIES IN CONSERVATION GENETICS IN TARPON (*MEGALOPS ATLANTICUS*) II. POPULATION STRUCTURE OF TARPON IN THE WESTERN GULF OF MEXICO

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## ABSTRACT

Previous studies employing genetic analyses found tarpon inhabiting the eastern and western Atlantic to be genetically isolated from tarpon from Costa Rica, the eastern Caribbean, and eastern Gulf of Mexico. Earlier work has not, however, examined tarpon from the western Gulf of Mexico. We collected data for tarpon from Mexico and Texas. The results of morphometric (length/weight allometries) and demographic analyses (sexual maturity and sex ratio) indicated no differences among samples obtained from fishing tournaments in the western Gulf and did not suggest any population subdivision in the Gulf of Mexico. However genetic analyses of these samples using allozymes and mitochondrial DNA restriction fragment length polymorphisms (RFLP) support the existence of at least two subpopulations in the western Gulf of Mexico. Genetic differences are discussed in the context of biogeographic patterns seen the Gulf of Mexico species.

## INTRODUCTION

Fisheries management attempts to balance short- and long-term goals for the exploitation of a resource. Rational management decisions may only be made when important aspects of the biology of the exploited species are known, including knowledge of population structure. Some species demonstrate population structures that are spatially and temporally homogeneous, while others are composed of discrete units that may respond differentially to exploitation (Allendorf et al. 1987). Short-term fisheries management strategies often ignore population-genetic information, focusing on readily collected morphometric and life-history data provided by local fisheries resources. This perspective can optimize immediate economical advantage, but can also have adverse implications for long-term management. Differential survival and reproduction of fish with different genotypes will potentially change the genetic composition of the exploited

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population resulting in loss of genetic resources, genetic integrity, and ability to adapt to changing environmental conditions. Rational management programs therefore give strong consideration to the genetic effects of management decisions. (Park and Moran 1995).

Highly migratory species that have larval stages with appreciable dispersal capacity have been the subject of detailed genetic studies (e.g., Buonaccorsi et al. 1999; Gold et al. 1997a; Gold et al. 1997b). It is often unclear if these species are genetically structured (Avise 1994). In addition to the mobility of adults and transport of eggs and larvae by oceanic currents (Gyllensten 1985; Ward et al. 1994), a lack of significant barriers to gene flow may explain the lack of genetic structuring among local demes of these species (Avise 1994).

Tarpon *(Megalops atlanticus)* is a euryhaline species widely distributed in the western Atlantic Ocean from the coast of Virginia in USA to Brazil, Venezuela, and Argentina, and throughout the Gulf of Mexico (Robins and Ray 1986). The early life of juvenile tarpon is spent in estuaries, lagoons, channels and other small bodies of water. Adult tarpon continue to inhabit coastal inshore waters and are presumed to be migratory (Zerbi, 1999). Spawning is constrained to offshore waters over abyssal depth in excess of 500 meters (FL Department of Environmental Protection, 1999). Although actual spawning grounds have not been identified, Crabtree et al. (1992) inferred the location of one such site (250 km from the coast) in the Gulf of Mexico west of Florida. The pelagic phase of the leptocephalus larva is estimated to last from 23-41 days (Cry, 1991). The larval migration process, which may take several months, is a passive one, subject to the effects of tides, currents, and wind direction (Chacón-Chaverri and McLarney, 1992). In Florida the larvae must travel more than 250 km before they reach the coastal areas (Cry, 1991).

Recreational exploitation of the tarpon in sport fisheries represents a valuable economic resource (Kowalsky 1987; McMillan-Jackson et al. 1993). However, many local fisheries targeting this species have collapsed. McMillan-Jackson and her colleagues (1993) conducted a study of morphometric and genetic characteristics of tarpon across much of the distribution of the species. The results of this study indicated that tarpon collected from Florida to Venezuela represented a single population lacking obvious structure. However, differences in allele frequencies at some loci and meristic counts suggest population subdivision, at least between Costa Rica and the Caribbean/Gulf of Mexico. Their study did not include the western Gulf of Mexico. The present study aims to examine population structure on a more detailed geographic scale, the western Gulf of Mexico.

## MATERIALS AND METHODS

### Morphometrics

Tarpon were captured by participants at a number of recreational fishing tournaments in 1998 (Table 1 and Figure 1). Specimens were measured (total length, TL), weighed, gonads were examined to determine sex and reproductive condition, and we determined the ratio of males to females. Sexual maturity was determined using the scale developed by Nikolsky (1963). The relationship between weight and length was calculated using the logarithmic equation detailed by Ricker (1975). Analysis of covariance was used to compare the slopes generated by this equation to differentiate among samples (Zar 1984) (Tampico $N = 5$; Tecolutla $N = 15$; and Veracruz $N = 32$).

### Genetics

Tissues from tarpon collected at five Mexican tournaments (Table 1 and Figure 1) were included in genetic analyses. Samples from additional Mexican tarpon were obtained in the summer of 1998 from a local fishing guide in Chetumal, Quintana Roo.

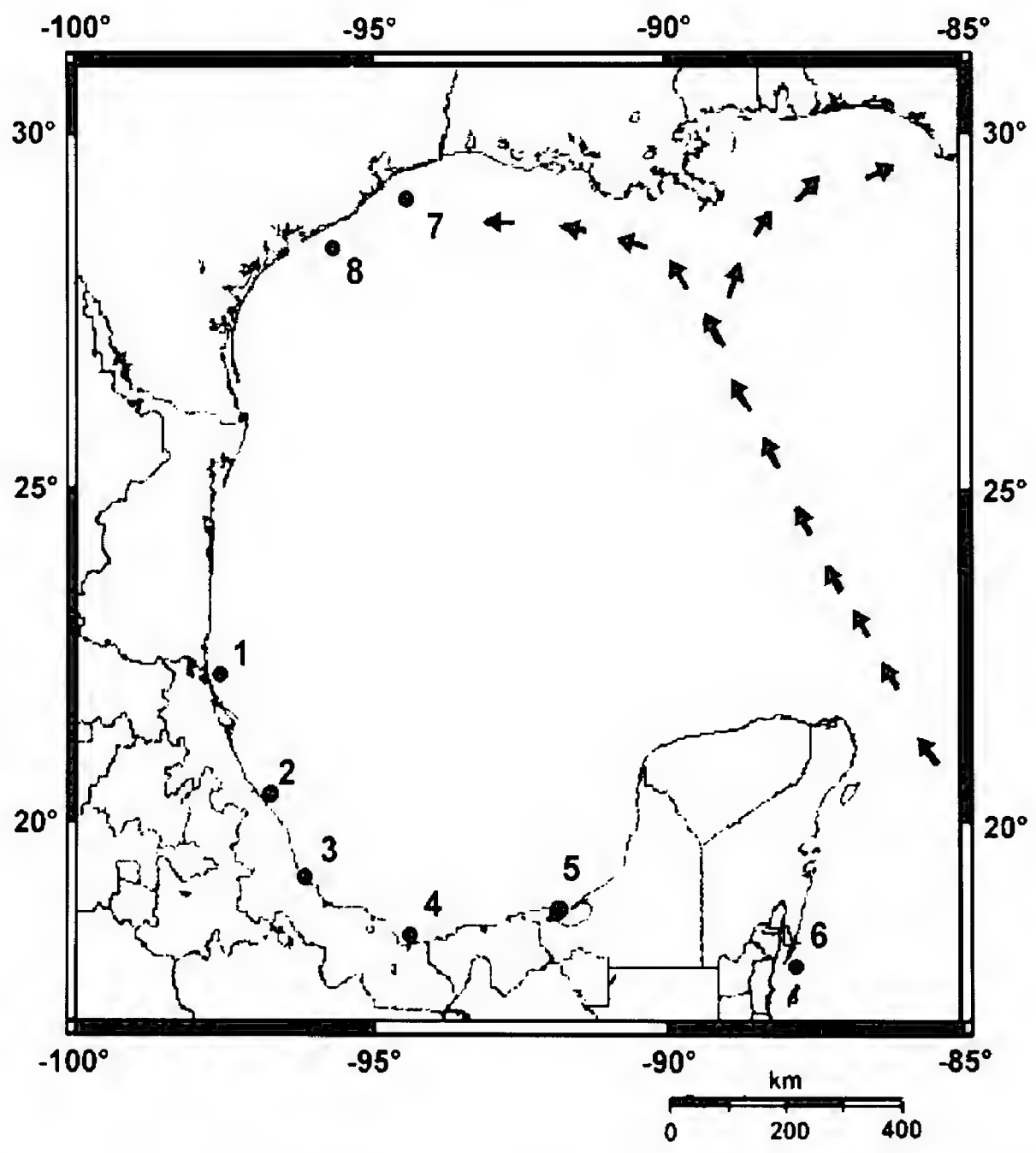


Figure 1. Sampling locations in the Gulf of Mexico. June current patterns are shown after Leipper (1945). Numbers refer to collecting localities defined in Table 1.

Texas tarpon were collected mostly from Texas Parks and Wildlife Department routine resource sampling during the spring and summer of 1998 and classified as 'Upper Texas Coast' if collected from Sabine Lake or Galveston Bay ($N$ = 8), and as 'Lower Texas Coast' if collected from Matagorda, San Antonio, Aransas, Corpus Christi Bay, or the Laguna Madre ($N$ = 32).

Table 1. Collection localities of Tarpon (*Megalops atlanticus*) used in various analyses of life history and genetic structure

| Locality | Date of Collection | N | Analyses | | |
|---|---|---|---|---|---|
| | | | Morphological | Allozyme | mtDNA |
| 1. Tampico, Tamaulipas | 27 June – 31 August | 6 | * | | * |
| 2. Tecolutla, Veracruz | 14 May | 15 | * | * | * |
| 3. Veracruz, Veracruz | 5 June | 33 | * | | * |
| 4. Coatzacoalcos, Veracruz | 31 August | 7 | * | | * |
| 5. Ciudad del Carmen, Campeche | 23 July | 4 | * | | * |
| 6. Chetumal, Quintana Roo | Summer | 18 | | | * |
| 7. Upper Texas Coast (Sabine Lake and Galveston Bay) | Summer | 8 | | * | * |
| 8. Lower Texas Coast (Matagorda Bay south) | Summer | 32 | | * | * |

## Allozymes

Skeletal muscle, liver, heart, and kidney tissues were excised from fresh or frozen fish from Tecolutla and some samples from Texas (Upper and Lower Coast). Sample preparation and electrophoretic techniques and conditions followed King and Pate (1992). Gel and electrode buffers used were: tris-borate-EDTA, pH 8.0 (Selander et al., 1971), tris-citrate, pH 8.0 (Selander et al., 1971), lithium hydroxide, pH 8.0 (Selander et al., 1971), borate buffer, pH 9.0 (modified from Sackler, 1966), and Poulik's discontinuous system, pH 8.7 (Selander et al., 1971). Histochemical methods were primarily taken from Manchenko (1994). Genetic nomenclature follows the suggestions

of Shaklee et al. (1990). Allele frequency distribution and genetic diversity indices, and estimated *F*-statistics were calculated according to Weir and Cockerham (1984) and Wright (1969) using the Genetix program (Belkhir et al. 1996-1998).

### Mitochondrial DNA

Muscle, fin, skin, and blood were sampled for DNA analysis (Upper Texas Coast $N = 6$; Lower Texas Coast $N = 32$; Tecolutla $N = 15$; Veracruz $N = 32$; and Chetumal $N = 18$). Tissues were preserved in 95% alcohol. Total genomic DNA was extracted using a Puregene® DNA isolation kit (Gentra Systems, Minneapolis, MN). A 1,900 bp mitochondrial DNA fragment was amplified spanning the small subunit ribosomal RNA (12S rRNA) and large subunit ribosomal RNA (16Ss rRNA) following protocols described in Hillis et al. (1996) using a Perkin-Elmer Gene Amp 2400 thermocycler programmed for 35 cycles at 94° C, 1 min; 48° C 1.25 min; and 72° C, 1.5 min. Amplifications were performed by combining approximately 80-100 ng of genomic DNA with Ready-to-Go™ PCR beads (Amersham Pharmacia Biotech, Inc., Piscataway, NJ) utilizing the following primers 5'-CCG GTC TGA ACT CAG ATC ACG T-3' and 5'-AAA AAG CTT CAA ACT GGG ATT AGA TAC CCC ACT-3'. Amplified samples were digested with twenty-six four-base and one six-base restriction enzymes following instructions specified by the manufacturer. Only three restriction enzymes were polymorphic (*Alu* I, *Mse* I and *Sau* 96 I). Restriction patterns were visualized on 2 % agarose gels.

Statistical analysis was performed on the following populations: Upper Coast and Texas (combining the Middle Coast, Lower Coast and the Lower Laguna Madre samples after finding no significant differences between the three groups mentioned above). Statistical analyses were performed with the statistical package Arlequin ver. 2.000 (Schneider et al. 2000), which was used to calculate haplotype frequencies and Wright's *F* values (1951). An unrooted neighbor-joining topology was constructed in Phylip (Felsenstein 1995) using the calculated $F_{ST}$ values of the different haplotypes [$D = - \ln(1-F_{ST})$].

## RESULTS

### Morphometrics

Morphometric data were recorded for 65 tarpon sampled during Mexican fishing tournaments (Table 2). Mean (± SD) total length (TL) was 1.94 ± 0.148 m and the average weight was 53.9 ± 13.2 kg. Size ranged from a 1.49 m male collected in Veracruz (weight not recorded) to a 2.26 m male weighing 73 kg collected in Tecolutla. The sex ratio was biased in favor of females in our sample. Fifty-three individuals were females (81.5%), 7 were males (10.7%) and 5 were undetermined (7.7%). The Veracruz sample had the highest proportion of females relative to males (15.5:1) followed by

Coatzacoalcos (5:1) and Tecolutla (2:1). No males were observed in Ciudad del Carmen and Tampico (Table 2).

Table 2. Total length (m, TL) and mass (kg, W) of tarpon (*Megalops atlanticus*) by study locality. Min = minimum; Mean = mean value; Max = maximum; SD = standard deviation; M = number of male; F = number of females; Ind = number of indeterminate individuals; A = number of mature (adult) individuals.

| Locality | | Min | Mean | Max | DS | M | F | Ind | A |
|---|---|---|---|---|---|---|---|---|---|
| Tampico | TL (m) | 1.77 | 1.83 | 1.89 | 0.047 | - | 5 | 1 | 3 F |
| *N* = 6 | W (kg) | 55.9 | 53.6 | 60.6 | 9.1 | | | | |
| Tecolutla | TL (m) | 1.69 | 2.01 | 2.26 | 0.141 | 4 | 8 | 3 | 1 F |
| *N* = 15 | W (kg) | 28.3 | 53.5 | 70.3 | 12.4 | | | | |
| Veracruz | TL (m) | 1.49 | 1.97 | 2.17 | 0.13 | 2 | 31 | - | 2 M |
| *N* = 33 | W (kg) | 37.0 | 57.7 | 79.0 | 13.9 | | | | 22 F |
| Coatzacoalcos | TL (m) | 1.60 | 1.82 | 1.99 | 0.139 | 1 | 5 | 1 | 2 F |
| *N* = 7 | W (kg) | 52.0 | 44.6 | 58.0 | 9.9 | | | | |
| Cd. Carmen | TL (m) | 1.70 | 1.74 | 1.80 | 0.045 | - | 4 | - | - |
| *N* = 4 | W (kg) | 39.4 | 41.4 | 42.2 | 1.34 | | | | |
| Global | TL (m) | 1.49 | 1.94 | 2.26 | 0.148 | 7 | 53 | 5 | 2 M |
| *N* = 65 | W (kg) | 28.3 | 53.9 | 73.0 | 13.2 | | | | 28 F |

The greatest percentage of mature fish (75%) were collected in Tampico in June of 1998. Veracruz in June 1998 also had a high proportion of mature individuals (73%) including fish found to be spent (10%). Only one mature female was observed in Tecolutla (May 1998), and only two in Coatzacoalcos (August 1998). All individuals sampled during the Ciudad del Carmen tournament (July 1998) were immature (Table 2). Sixty-five individuals were used to obtain the following length-weight relation:

$$\text{Log (W)} = 0.9897 + 2.5667 \text{ (TL)}.$$

The slope value of this ratio was similar among the Veracruz (*N*=33), Tecolutla (*N*=15), and Tampico (*N*=6) populations (Ho: $b_1=b_2=b_3$); $P > 0.05$).

## Allozymes

A total of 31 individuals yielded results from two collection areas, Texas (N = 16) and Tecolutla (N = 15) (Table 1). Consistently scorable expression patterns were resolved for five loci (Table 3). Allele frequencies for each of the five loci varied between the two populations, however in each case the same allele was most frequent in both populations . Two loci, *LDH*-1*100 and *LDH*-2*100, were fixed in the Tecolutla sample. The Texas

Table 3. Allele frequency distribution and mean number of alleles per locus per population obtained from 5 polymorphic loci in tarpon (*Megalops atlanticus*) in Texas and Tecolutla, Mexico.

| Locus / Locality | Texas<br>$N = 16$ | Tecolutla<br>$N = 15$ |
|---|---|---|
| *MPI** | | |
| *1 | 0.375 | 0.066 |
| *2 | 0.625 | 0.933 |
| *LDH-1** | | |
| *1 | 0.115 | 0 |
| *2 | 0.884 | 1 |
| *LDH-2** | | |
| *1 | 0.785 | 1 |
| *2 | 0.214 | 0 |
| *G3PDH-1** | | |
| *1 | 0.333 | 0.100 |
| *2 | 0.666 | 0.900 |
| *PEPB** | | |
| *1 | 0.366 | 0.033 |
| *2 | 0.600 | 0.966 |
| *3 | 0.033 | 0 |
| Mean number of alleles | 2.2 | 1.6 |

sample expressed three alleles, *LDH*-1*90, *LDH*-2*110, and *PEPB**90, which were absent in the Tecolutla sample. Observed mean heterozygosity was higher in Texas tarpon ($\overline{H} = 0.40$) than in Tecolutla fish ($\overline{H} = 0.08$). All loci were in Hardy-Weinberg equilibrium for both populations ($F_{IS} = 0.009$, $P > 0.05$ for Texas; $F_{IS} = -0.05$, $P > 0.05$ for Tecolutla). However, when the samples were combined a deficit in heterozygosity was observed ($F_{IT} = 0.199$, $P = 0.001$). The genetic differentiation test utilizing $F_{ST}$ found the two populations to be significantly different ($F_{ST} = 0.199$, $P = 0.001$).

## Mitochondrial DNA

Three restriction enzymes, *Alu* I, *Mse* I, and *Sau* 96 I, produced patterns interpreted to be polymorphic and consistently scorable when applied to the 12S-16S rDNA fragment. The *Alu* I digest yielded 2 haplotypes distinguished by a shift in 1 of 4 observed bands. Two haplotypes were also observed in the *Mse* I digest. The *Sau* 96 I digest yielded 3 banding patterns. Five composite haplotypes were observed across the extent of the study (Table 4). Differences were found among tarpon in the western Gulf of Mexico, with tarpon from the upper Texas coast being most distinct. Composite haplotype 1 was most common, or tied for most common, in all samples. Only composite haplotype 2 was

Table 4. A. Restriction fragment sizes in number of base pairs. B. Restriction patterns of composite haplotypes (presence and absence of fragment size) obtained from the subunits 12S rRNA-16S rRNA in mt-DNA of (*Megalops atlanticus*) collected in different locales of the Gulf of Mexico.

A.

| *Alu* I | *Mse* I | *Sau* 96I |
|---|---|---|
| 517 | 1605 | ~700 |
| 460 | ~1000 | ~680 |
| ~400 | ~420 | ~370 |
| 350 | 396 | ~230 |
| ~230 | | |
| ~220 | | |

B.

| Haplotypes | Restriction Pattern | | |
|---|---|---|---|
| | *Alu* I | *Mse* I | *Sau* 96I |
| 1 | 11101 | 1001 | 001 |
| 2 | 11101 | 1110 | 001 |
| 3 | 11101 | 1001 | 100 |
| 4 | 11101 | 1001 | 101 |
| 5 | 11011 | 1001 | 001 |

confined to a single site. Of special interest is composite haplotype 5 which shows a clinal change, increasing in frequency from north to south in the western Gulf of Mexico (Table 5).

The measures of inter-population genetic variability indicate that tarpon populations show structure across their distribution in the Gulf of Mexico, with the upper coast population showing the greatest differentiation with respect to the rest of the sample. We obtained low values of effective migrants between tarpon from the upper Texas coast and demes further south in the Gulf of Mexico (Table 6). Similarly, we found statistically significant distance values between tarpon from the upper Texas coast and the lower Texas coast ($D = 0.250$, $P = 0.05$), Veracruz ($D = 0.295$, $P = 0.05$), and Chetumal ($D = 0.326$, $P = 0.05$). The topology of the unrooted tree obtained with the neighbor-joining method using genetic distances (Figure 2) indicated that the upper Texas coast is clearly distinct from other samples in the western Gulf of Mexico.

Table 5. Haplotype frequencies obtained from the 12S rRNA-16S rRNA subunits in tarpon mtDNA in 5 locales in the Gulf of Mexico.

| | Upper Texas Coast N=6 | Lower Texas Coast N=32 | Tecolutla N=15 | Veracruz N=32 | Chetumal N=18 |
|---|---|---|---|---|---|
| Haplotype 1 | 0.500 | 0.875 | 0.733 | 0.812 | 0.778 |
| Haplotype 2 | 0 | 0 | 0.066 | 0 | 0 |
| Haplotype 3 | 0 | 0.062 | 0.066 | 0 | 0 |
| Haplotype 4 | 0.500 | 0.031 | 0.066 | 0.031 | 0 |
| Haplotype 5 | 0 | 0.031 | 0.066 | 0.156 | 0.222 |

Table 6. Effective number of migrants *Nm* (above diagonal) and $F_{ST}$ values (below diagonal) between populations based on RFLPs from 5 localities in the Gulf of Mexico. ** $P = 0.01$; * $P = 0.05$.

| | Upper Texas Coast | Lower Texas Coast | Tecolutla | Veracruz | Chetumal |
|---|---|---|---|---|---|
| Upper Texas Coast | - | 1.76 | 8.83 | 1.45 | 1.30 |
| Lower Texas Coast | 0.221* | - | ∞ | 11.18 | 4.25 |
| Tecolutla | 0.054 | -0.021 | - | 47.54 | 14.33 |
| Veracruz | 0.256** | 0.043 | 0.010 | - | ∞ |
| Chetumal | 0.278* | 0.105 | 0.034 | -0.029 | - |

## DISCUSSION

### Morphometrics

The Mexican samples utilized in this study were collected during sport fishing tournaments where the main goal is to obtain the biggest fish possible. This biased our sample towards large fish and away from other size classes including sub-adults (>1.0 m). It was not possible to identify spawning areas, however gonad development data indicated sexually mature fish were present in the sampled area during the months of May-August, reaching a peak during the month of June. Spawning in Florida occurs from May to July (Crabtree et al. 1995), in Puerto Rico it extends from March to August (Figuerola 1996), while in Costa Rica it occurs throughout the year (Crabtree et al. 1997). These differences in the spawning period could indicate regionally different tarpon stocks.

The bias in sex ratio toward females observed in this study may be an artifact of targeting large fish by tournament fishermen. However, it is also possible the bias may

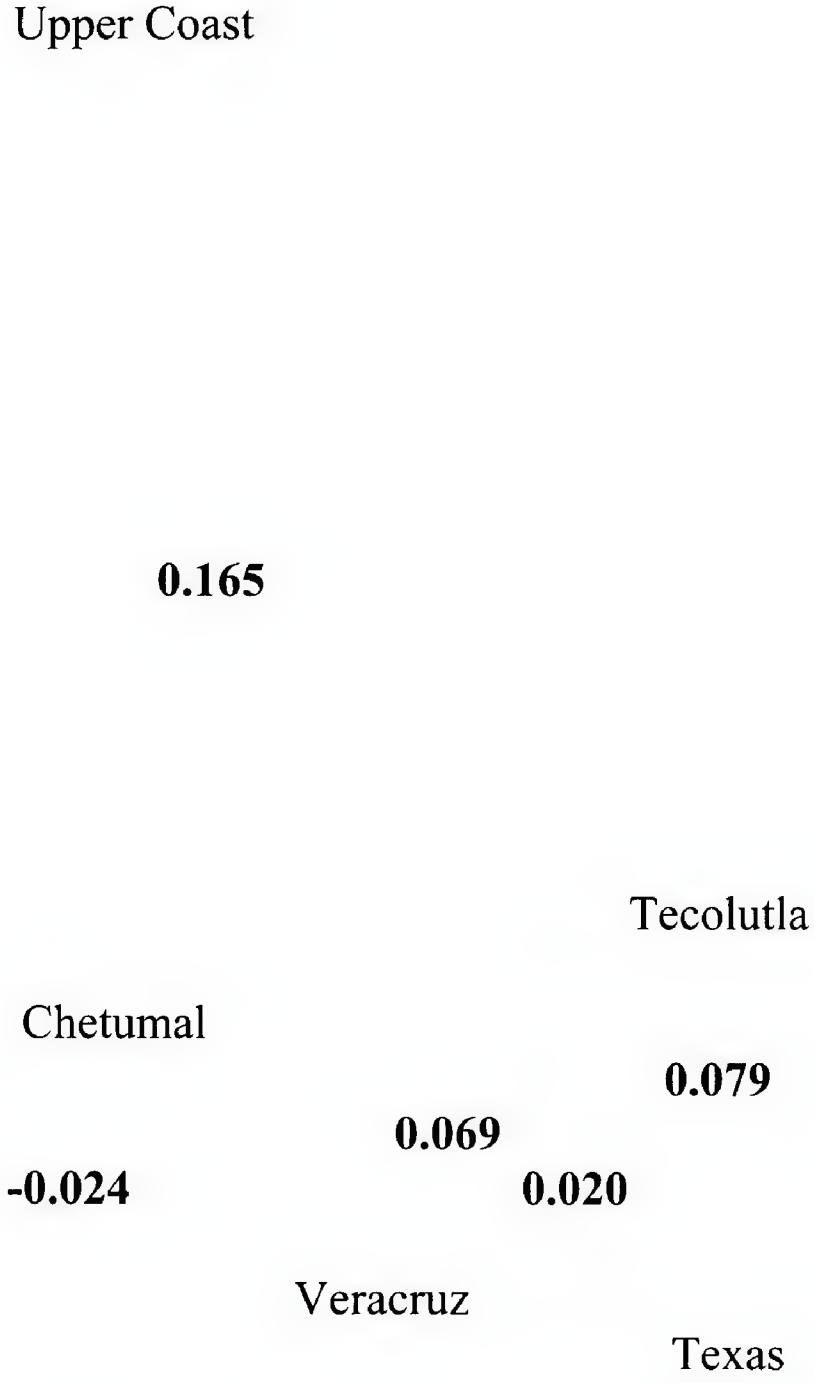


Figure 2. Unrooted neighbor-joining tree of tarpon collected at five Gulf of Mexico localities, based on RFLP analysis of 12S rRNA-16S rRNA subunits. Numbers indicate branch length.

indicate differential migration of male and female segments of the population. In several other species, separate migration of the sexes during pre-reproductive periods is followed by congregation in areas where both sexes aggregate for spawning activities (Dingle 1996).

## Allozymes

Allozymic polymorphism expressed in number of alleles per locus, average number of alleles per locus per population, and average heterozygosity all indicated that the Texas sample was more diverse than tarpon from Tecolutla. The differences observed at the *PEPB** locus, with Texas having 3 alleles compared with 2 for Tecolutla could indicate genetic differences between populations. Also of interest was the presence of fixed alleles at both *LDH** loci in the Tecolutla sample. Genetic variability levels reported in this

study for allozymes are high ($\overline{H}$ = 0.407 for Texas and $\overline{H}$ = 0.076 for Tecolutla) relative to other marine fish species. Mean heterozygosities estimated for marine teleosts averaged 0.055 (Smith and Fujio 1982) with 0.063 for marine species in general (Gyllensten 1985) and 0.064 for temperate pelagic fish species (Ward et al. 1994). However, heterozygosity levels similar to the ones obtained for tarpon have been observed in Atlantic herring (*Clupea harengus*, $\overline{H}$ = 0.360) (Gyllensten 1985). Heterozygosity observed in Tecolutla was similar to the values reported by McMillan-Jackson et al. 1993 for tarpon from eastern Florida and for the species *Lythrypnus dalli* from California and Baja California ($\overline{H}$ = 0.074 and 0.087 respectively).

The $F_{IS}$ value for both populations was almost 0, indicating both the Texas and Tecolutla populations were in Hardy-Weinberg equilibrium. The $F_{IT}$ value was significantly different from 0, suggesting that genetic variability could be a Wahlund effect due to the presence of reproductive sub-units inside the sample that are present but non-detectable with the Wright index (García de León et al. 1997). Indeed the $F_{ST}$ value was highly significant ($F_{ST}$=0.199; P<0.001) showing that populations are different from one another. Based on allozyme data, the genetic distance between Texas and Tecolutla tarpon was high ($D$ = 0.221). Similar values have been obtained for tarpon populations from geographically distant locales such as eastern Florida versus Costa Rica Coast, and west Africa ($D$ = 0.219 and 0.225, respectively; McMillan-Jackson et al. 1993) and for the woolly sculpin (*Clinocottus analí*) from California versus Baja California ($D$ = 0.246; Waples 1987).

Under the infinite islands model, the estimated number of migrants between the upper Texas coast and Tecolutla (*Nm*) is 1.01, suggesting gene flow between the regions is low. In light of this interpretation, long-term (evolutionary) and short term (ecological) consequences may be examined. If we suppose that effective population size is approximately 50,000 individuals, similar to the 37,000 estimated for European sea bass (García de León et al. 1997), a species with life history parameters similar to tarpon, the percentage of individuals exchanged between populations (*Nm/N*) may be estimated to be about 0.002 %. This means that Texas and Tecolutla tarpon function as two independent stocks. In differentiating stocks, fisheries biologists are interested in *m* while geneticists are interested in *Nm*. In the case of tarpon, both values suggest Texas and Tecolutla populations function as two independent units.

Mitochondrial DNA

Intrapopulation analyses of mt-DNA genetic polymorphism detected by analysis of PCR/RFLP found haplotype 1 to be present in all populations, though at variable frequencies. Tecolutla was the most diverse population and was the only one where all five composite haplotypes occurred. The mtDNA analyses agreed with the genetic

differentiation revealed by allozymes data. The $F_{ST}$ values among the five populations studied showed clear differentiation between the upper Texas coast and the other populations. Statistically significant $F_{ST}$ values were found for the upper Texas coast relative to the rest of Texas ($F_{ST}$ = 0.22; P = 0.05), Veracruz ($F_{ST}$ = 0.26; P = 0.01), and Chetumal ($F_{ST}$ = 0.28; P = 0.05). Similarly, genetic distance ($D$) values were statistically significant for upper Texas coast versus the rest of Texas ($D$ = 0.250, P = 0.05); Veracruz ($D$ = 0.295, P = 0.05); and Chetumal ($D$ = 0.326, P = 0.05). Comparable genetic distance values have been observed using PCR/RFLP of mtDNA analyses for other species with populations distributed from Florida to Texas such as red snapper (*Lutjanus campechanus*, $D$ =0.2360; Gold et al. 1997b).

As in the allozyme study, mtDNA estimates of effective numbers of migrants between the upper Texas coast and the other populations in Texas, Veracruz, and Chetumal were small ($Nm$=1.76, 1.45 and 1.3 respectively). These values of $Nm$ have the same implications of low gene flow that were noted in the discussion of variation of allozymes. The un-rooted tree showed a clear separation of the Upper Texas Coast from the other samples, confirming that this population is genetically distinct.

The results obtained in this study differ from the results reported by McMillan-Jackson et al. (1993) which indicated little evidence of genetic structure among tarpon populations from the Atlantic Ocean utilizing the same type of genetic markers, or by Blandon et al. (2002) whose examination of variation in PCR/RFLP of tarpon across its distribution found few differences except in isolated demes. The genetic structure discerned in the present study has been found in a smaller geographical scale, in the western Gulf of Mexico off the coasts of Texas and Mexico.

Despite the small sample size for both genetic markers included in this study, and the apparent contradiction between genetic diversity between the "northern and southern" tarpon populations from Texas and Mexico as discerned by the two markers, the results are consistent, with both types of genetic markers indicating a genetic structure of tarpon populations. The data clearly indicate at least two tarpon populations in the Gulf of Mexico, a northern and a southern. These populations are most likely separated by an ocean current that flows from northeast and bifurcates the east and west of the Gulf of Mexico. Water enters the Gulf of Mexico through the Yucatan Channel, then separates into several lesser currents. The main current goes across the center of the Gulf and bifurcates into two dominant currents off the coast of Louisiana and Mississippi, one turning to the east, the other to the west of the Gulf (Leipper, 1954). These currents in the Gulf of Mexico may act as a barrier to dispersal between larvae of two populations of tarpon in the Gulf of Mexico. Individuals sampled on the upper Texas coast populations may be from a population distributed from the upper Texas coast to Florida. This

population may not mix with individuals from lower on the Texas coast or from the Mexican coast.

In the Gulf of Mexico, several species have been reported to have similar population structure geographically concordant with the one we report for tarpon. Burns and Nakamura (1988) observed genetic variation in two alleles in the *PEPA**2 locus of *Scomberus cavalla* confirming the existence of two stocks of this species in the Gulf of Mexico; one for the eastern Gulf and another for the western Gulf of Mexico. Burns and Nakamura (1988) also confirmed the occurrence of two populations of mackerel (*Scomberus maculatus*) in the Gulf of Mexico, with one population resident in Florida and Mississippi and the other population from Louisiana, Texas, Tamaulipas, and Yucatan. This type of population structure has also been detected in the crustacean *Alpheus angulatus* (McClure and Greenbaum 1999) and in the mollusc *Argopecten irridians* (Wilbur and Gaffney 1997). The genetic structure evident in all these species may be explained by current patterns providing a geographic barrier preventing the dispersal of larval and/or juvenile stages similar to our hypothesis concerning tarpon. The 'northeastern Gulf tarpon population' may have an origin on the Florida coast. Florida has been identified as a major spawning ground for this species (Smith 1980; Crabtree et al. 1992)). Tarpon larvae develop near the Florida coast even though they are pelagic and can be transported by the currents up to 250 km (Cry, 1991). During the tarpon's spawning period the current pattern in front of the coast of Florida changes to a gyre (Leipper 1954) preventing dispersal of larvae west of the Mississippi coast (Crabtree et al. 1995). Known spawning grounds for tarpon are located in the eastern Gulf of Mexico along the Florida coast and in the western Gulf from Veracruz southward (Smith 1980), providing possible recruitment sources for the two putative stocks. However, adults have the potential to migrate long distances. In the face of this potential for movement by adults behavioral constraints promoting philopatry are necessary to maintain isolated populations (Avise 1994). This hypothesis needs to be tested with a larger sample size collected from numerous collection sites and utilizing highly polymorphic genetic markers such as microsatellites.

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# RECORDS OF *MEGALOPS ATLANTICUS* ON THE MEXICAN CARIBBEAN COAST

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## ABSTRACT

Preliminary information is presented on occurrence and use of tarpon in cenotes (karstic sinkholes) in central Quintana Roo, Mexican Caribbean versant, as well as records of larvae, juveniles and adults in reefs, lagoons and wetlands along this coast. Tarpon, locally known as "sábalo", have been recorded in three cenotes within Sian Ka'an Biosphere Reserve, central Quintana Roo. One of these is a small anchialine water body, with subterranean tidal influence, where only tarpon juveniles have been caught. The other two are large freshwater cenotes, several kilometers away from the sea, seasonally connected to the Caribbean through sawgrass marshes and similar habitats; here adults were observed in schools of 6-12 individuals. People in the Mayan villages near Sian Ka'an fish tarpon for local consumption with hook and line during the dry season, when these cenotes are reachable by foot and tarpon become isolated. Tarpon larvae are rare in ichthyoplankton collections. In the Mexican Caribbean, a few 24-mm-long leptocephali have been collected in December and August between Puerto Morelos and the Belizean border. These scant data are nevertheless enough to suggest that tarpon may have a more extended reproductive season in Quintana Roo than in Florida and Brazil. Juvenile and adult tarpon have also been reported from the Hondo River and small coastal lagoons in the southern coast of Quintana Roo. Large schools of adults are common in Chetumal Bay and in the reef off the southern coast, especially at a drop-off called "La Poza" near Xcalak. Tarpon sustains a moderate sport fishery in these coastal lagoons and in Chetumal Bay, as well as in Holbox and Punta Allen.

## INTRODUCTION

Mexico's Caribbean versant lies within the state of Quintana Roo, the oriental third of the Peninsula of Yucatan, within parallels 17°48' and 21°10'N. There are no significant altitude variations; Zohlaguna Plateau, at the southwestern tip of the state, in the limit with the El Petén department of Guatemala, reaches 380 m above sea level, but almost all water bodies in Quintana Roo are no higher than 20 m. The relief is nearly level, except

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near the upper Hondo river (border between Mexico and Belize) and along the ancient Pliocene coast, about 100 km from the present shoreline.

Freshwaters in Yucatan are hard, because of limestone. In cenotes close to the sea (< 2 km) there often is a seawater layer near the bottom (Iliffe, 1992). Temporary lakes display ecological succession phases depending on the rains (Arredondo-Figueroa & Flores-Nava, 1992); permanent lakes can increase their surface area 150% between seasons.

All along this coast, the world's second largest barrier reef stretches from Belize and extends to Honduras. Its development depends on the influence of freshwater from the land. In the central coast of Quintana Roo, where there are two large, mangrove-bordered bays, the reef crest lies about 2 km from the beach, whereas in other localities it can be as close as 250 m. In some places the barrier is interrupted by channels. Between the reef and the coast, the reef lagoon, often with sea-grass meadows (mainly *Thalassia testudinum*), links mangrove and coral reef habitats. Seawater flows northwards, as a continuation of the Caribbean current, coming from northern South America; however, promontories and bays deflect part of the flow and originate coastal countercurrents, oriented southwards (Merino Ibarra, 1986).

The only river in the area, the Hondo, empties into Chetumal Bay, which itself meets the Caribbean through several narrow channels. The bay does not have estuarine dynamics, and its brackish salinity is fairly constant throughout the year (Pimentel, 2001).

Several tarpon stages have been recorded in many of the aforementioned habitats. In this paper our objective is to present and discuss tarpon occurrence, including larvae, juveniles and adults, in Mexico's Caribbean coast, inferring abundance when possible.

## METHODS

We obtained tarpon records from four main sources: a study on tarpon and its use in the cenotes of Sian Ka'an Biosphere Reserve, central Quintana Roo (Arce-Ibarra, 2000), an inventory of continental fishes of Quintana Roo (Schmitter-Soto, 1998), a checklist of marine fishes of the Mexican Caribbean (Schmitter-Soto et al., 2000), and ichthyoplankton surveys (Smith, 1980; Vásquez-Yeomans et al., 1998; Pereyra, 2001; Schmitter-Soto et al., 2001).

Between April 1998 and December 2000, fish species composition was studied in permanent ponds and cenotes of central Quintana Roo. Tarpon, cichlids and sleepers found in these environments are a fishing resource for rural communities. We used hook-and-line gear to catch tarpon, and tarpon school movements were annotated through visual observations.

During the freshwater fish inventory, conducted between 1992 and 1998, Quintana Roo was stratified into ten subareas, where similar sampling efforts were applied. Water bodies (permanent lakes, cenotes and wetlands) were visited at least twice, in different seasons (rainy, dry and 'north winds' seasons, Merino Ibarra, 1986). Of the diverse fishing gear used to capture tarpon, gillnets, seine nets, visual observations, and commercial or sport capture review were the most productive approaches.

Tarpon leptocephali were collected in nearshore Mexican Caribbean waters (2-4 m deep) using a standard plankton net (0.5 m mouth-opening, 0.5 mm mesh) towed for 10 minutes in a circular pattern near the surface, and a sled sampler (70 x 40 cm and 0.5 mm mesh) towed for 15 minutes in a horizontal pattern near the bottom (25 cm). All collections were made at night (20:00-05:30). Collected specimens and environmental data were prepared and stored at the fish and ichthyoplankton collections at ECOSUR (ECO-CH P, ECO-CH LP, respectively).

## RESULTS

Fifteen sites (four permanent lakes and 11 cenotes) were sampled in central Quintana Roo. Tarpon were recorded in only two of them, the freshwater cenotes Kan Dzonot and Noh Dzonot, located in the wetlands of the Sian Ka'an Biosphere Reserve (Fig. 1). Tarpon were observed at these cenotes during three consecutive dry seasons (1998 to 2000). Adults and subadults were seen moving around these two cenotes forming schools of 6-12 individuals. On three occasions three tarpon subadults were caught (standard lengths 740 mm, 568 mm, and 790 mm).

During the inventory of continental fishes, 240 water bodies were explored. Juvenile and adult tarpon were recorded in only seven of them. The complementary data from the checklist of marine fishes in the Mexican Caribbean yielded three additional sites (Fig. 1). An anchialine cenote near Tulum (Navarro-Mendoza, 1988) and the mangroves of Sian Ka'an had only juvenile tarpon. Adults were observed or caught in coastal lagoons (Boca Paila, Río Huach); the Hondo River, about 20 km away from Chetumal Bay; Chetumal Bay itself, where a 1.90 m individual was caught off Chetumal City harbor; the southern third of the reef barrier, at Mahahual and especially at a drop-off called "La Poza", near Xcalak; and in insular lagoons (e.g. Makax lagoon in Isla Mujeres).

Twenty-two tarpon leptocephali were collected during the study period in three localities; 21 with the standard plankton net and only one with the sled sampler. One larva was collected at Mahahual, one at Punta Allen (Sian Ka'an) and the remainder at Bacalar Chico (Fig. 1). Leptocephali ranged 21.3-24.0 mm SL (mean 23.0 mm, 0.8 S.D.) (Table 1). All larvae collected corresponded to developmental stage I (Wade, 1962). An additional larval record was given by Ordóñez-López (2001), off Puerto Morelos, northern Quintana Roo.

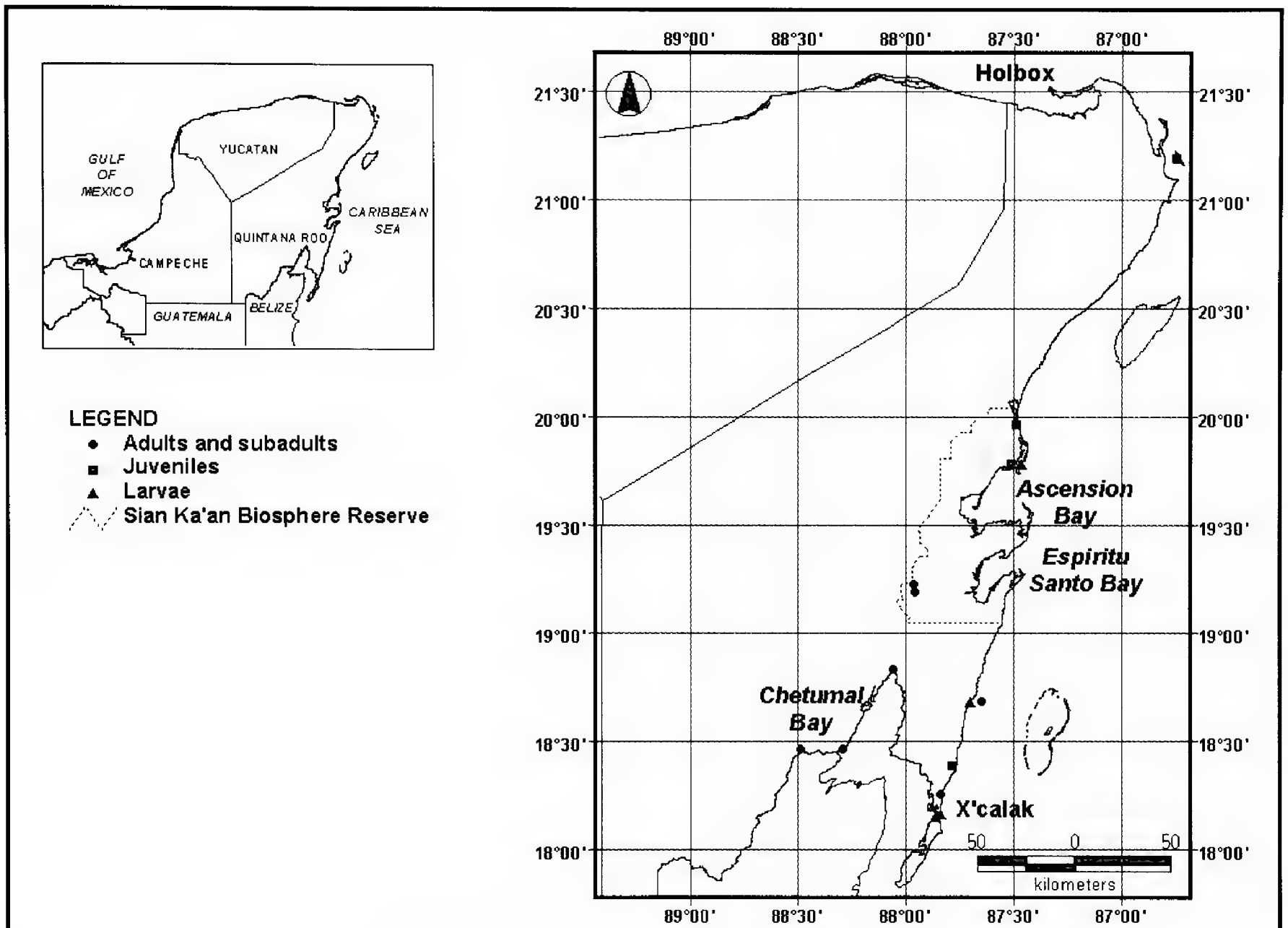


Figure 1. Tarpon records in the Mexican Caribbean. See Table 1 for further data.

Table 1. Tarpon records in the Mexican Caribbean. Catalog numbers refer to fish (P) and ichthyoplankton (LP) collections at ECOSUR. Not included are sightings of large adults on the reef at Mahahual, the Hondo River and Río Huach Lagoon.

| **Cat. No.** | **Locality** | **Coords.** | **Date** | **Time** | **SL (mm)** |
|---|---|---|---|---|---|
| LP 2716 | Reef at Mahahual | 18° 42' 54"N 87° 40' 50"W | 31/12/90 | 19:00 | 23.0 |
| LP 2717 | Bahía Ascensión | 19° 49' 12"N 87° 27' 19"W | 21/08/98 | 04:58 | 23.5 |
| LP 1782, 1995, 2718 | Bacalar Chico | 18° 11' 49"N 87° 50' 49"W | 7/12/99<br>8/12/99<br>6/12/98 | 02:21<br>01:09<br>03:25 | 22.0-24.0 |
| LP 2719-2722 | Bacalar Chico | 18° 11' 49"N 87° 50' 49"W | 23/06/98 | 01:22<br>02:00<br>02:22<br>05:30 | 21.3-24.0 |
| LP 2321, 2693 | Bacalar Chico | 18° 10' 58"N 87° 51' 26"W | 31/07/00<br>2/08/00 | 22:00<br>23:35 | 23.0-23.5 |
| P 3680, 4690 | Noh Dzonot | 19° 15' 40"N 87° 57' 15"W | 26/05/99<br>31/03/00 | 12:20<br>06:20 | 740-790 |
| P 4659 | Kan Dzonot | 19° 13' 28"N 87° 57' 09"W | 29/03/00 | 10:38 | 568 |
| P 2207 | Isla Mujeres, inland waters | 21° 13' 17"N 86° 43' 56"W | 10/01/98 | - | 92.6-110.8 |
| P 2688 | Mangrove at Vigía Chico | 19° 49' 25"N 87° 30' 00"W | 15/02/95 | 08:25-08:45 | 140.0-155.0 |
| P 3139 | Río Krik | 18° 45' 00"N 88° 02' 30"W | 8/12/92 | 13:00 | 381.0 |
| P 4381 | Chetumal City harbor | 18° 29' 57"N, 88° 17' 00"W | no precise date, 1992 | - | 1900.0 |

## DISCUSSION

Tarpon inhabit Mexico's Caribbean waters and adjacent rivers, bays and cenotes. The first report of tarpon at cenotes was done by Navarro-Mendoza (1988), in Cenote Salvaje, central Quintana Roo. Kan Dzonot and Noh Dzonot were discovered as new localities by Rojas-García (1999). Given that these cenotes are located within wetlands, entrance by foot to the area is possible only during the dry season, between February and May. People from the Mayan villages near Sian Ka'an fish tarpon with hook and line for self-consumption in that season. To our knowledge, no other records of tarpon from cenotes have been made before. The range of sizes recorded at these cenotes is similar to the range at Sebastian River (Crabtree et al., 1995) on Florida's Atlantic coast. In contrast, size distribution at Colorado River, Costa Rica (Chacón-Chaverri, 1993), where a sport fishery is settled, is apparently bimodal; only juveniles (< 260 mm SL) and adults (> 845 SL) were caught.

To explain in detail the mechanism whereby tarpon reach cenotes from the Sian Ka'an Biosphere Reserve, we would need data regarding drainage dynamics of this region. We know that these water bodies are connected during the rainy season to the Caribbean Sea through sawgrass marshes and similar habitats. For other habitats in the Atlantic coast, where an inland migration of tarpon has been reported, Loftus and Kushlan (1987) mentioned that "tarpon penetrates the Everglades region by using canals during high-water periods"; however, they also reported that "tarpon apparently can move across inundated marshes to reach deeper bodies of water" much farther inland. Richards (1968) found juvenile tarpon in both lotic and lentic waters (pools and creeks) in Georgian salt marshes, isolated from the sea except during the highest tides or storms. The same mechanism might explain their presence in the cenotes of Yucatan. Most cenotes in Sian Ka'an Biosphere Reserve may be reached this way during the rainy season, albeit some of them only during wetter cycles. Others, closer to the sea, have underground tunnels, which provide another entrance.

The Caribbean coast of Mexico seems to be an important spawning area for tarpon. Smith (1980) confirmed this by collecting 31 very small larvae from 20 tows off Cozumel in 1975 and 1977, and others collected off Banco Chinchorro. Previous studies have indicated that tarpon spawn in the spring and summer, although Smith (1980) suggested that spawning may begin earlier in the Caribbean, based on the presence of a 21-mm specimen off Cozumel in April (ANSP 156083). Hildebrand (1963) reported finding nearly ripe tarpon in the Panama Canal Zone from February to April and theorized that at least some spawning takes place at that time. Leptocephali records presented in this study were collected in the three local seasons (dry, rainy and 'north winds'). However, fourteen larvae occurred at the end of the dry season (June) and four in the rainy season (July and August), coinciding with the finding by Smith (1980), while

the others were collected in December ('north winds' season). The latter larvae could come from local spawning tarpon populations or currents from spawning areas farther south may have carried them. Crabtree et al. (1992) and Crabtree (1995) found that Florida tarpon spawning is seasonal and occurs after a long migration offshore during May-August. This was confirmed by Crabtree et al. (1997), who also found that tarpon spawning in Costa Rican waters occurred throughout the year. De Menezes and Paiva (1966) found that tarpon reproduction occurs during October-January off the northeastern coast of Brazil. We conclude that for Mexican Caribbean water tarpon have more than one reproductive season, perhaps with a peak in June-August. The data presented here are scant, but seem to support this assertion.

We found that this species supports two types of fisheries in Quintana Roo, Mexico. The first one is a sport fishery that takes place at Holbox, Espíritu Santo Bay (A. Arellano-Guillermo, pers. comm.), de la Ascensión Bay, Chetumal Bay (Camarena and Cobá, 1991), and off the southern coast of Quintana Roo (Xcalak). In Xcalak, tarpon may also be incidentally caught in gillnets (Sosa-Cordero et al., 1991). The second type is the artisanal fishery, mainly used for self consumption, in Chetumal Bay (D. Rovelo, pers. comm.) and at the cenotes of Sian Ka'an Biosphere Reserve.

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# FEEDING BEHAVIOR AND PREY CAPTURE KINEMATICS OF JUVENILE TARPON (*MEGALOPS ATLANTICUS*)

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## ABSTRACT

Tarpon, *Megalops atlanticus*, inhabit estuarine and coastal waters and support an economically important sport fishery. Tarpon are primarily predatory fish, feeding mostly on fish and crustaceans. This study was designed to investigate the kinematics and behavior involved in the feeding repertoire of tarpon. Four juvenile tarpon were filmed in the laboratory using a high-speed video system while feeding on mosquitofish. Tarpon fed aggressively; prey was always approached from underneath, captured with the oral jaws, and swallowed whole. The kinematics of a prey capture cycle in tarpon is characterized by two major events: (1) a rapid expansive phase involving postero-dorsal cranial rotation, hyoid depression, and mouth opening that occur during the first third of the cycle as the prey is being captured; and (2) a slower compressive phase involving antero-ventral rotation of the head, hyoid elevation, and closing of the mouth to swallow prey. We hypothesize that buccal expansion during prey capture is facilitated primarily by the extreme ability of tarpon to rotate its cranium postero-dorsally. Knowledge of the behavior and kinematics of prey-capture in tarpon is important in light of our continuing search for information that elucidates our understanding of the physiological and behavioral mechanisms that underlie the ability of these fish to utilize different habitats through ontogeny.

## INTRODUCTION

Tarpon, *Megalops atlanticus*, are a favorite target of sport fishermen in Florida and parts of the Caribbean because they strike hard at lures and baits, and challenge the angler by making strong runs that result in spectacular airborne displays (Cyr 1991). *M. atlanticus* is distributed along coastal waters of the tropical and subtropical western Atlantic Ocean, ranging from Virginia to Brazil and the Gulf of Mexico, and eastern Atlantic off tropical Africa (Zale and Merrifield 1989; Cyr 1991). They are most abundant along the coasts of the West Indies, Florida, and the Gulf of Mexico and they

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support an economically important recreational fishery in these regions (Zale and Merrifield 1989; Crabtree et al. 1995). Although *M. atlanticus* occur in a variety of habitats including lakes, rivers, and offshore marine waters, the population that supports the recreational fishery includes fish that are found mostly in estuarine and coastal habitats (Crabtree et al. 1995). Juvenile tarpon also occur in small stagnant pools and sloughs that have a wide range of temperature, salinity, pH, and oxygen concentration (Wade 1962).

In estuarine and other coastal habitats tarpon forage on zooplankton, insects (aquatic and terrestrial), fishes (poeciliids, cyprinotontids, and mugillids), crabs, plant remains, waste matter and grass shrimp (Harrington and Harrington 1960; Catano and Garzon-Ferreira 1994; Chacon 1994). Tarpon are typically crepuscular and nocturnal feeders (Robins and Ray 1978). Aside from this descriptive information on the food habits of *M. atlanticus*, our understanding of the feeding behavior of this species is lacking. This study is the first to investigate the behavior and kinematics of feeding in *M. atlanticus* using high-speed videography. Direct observation of tarpon feeding using high-speed videography is important for several reasons. First, an understanding of the interaction between tarpon and its prey benefits greatly from high-speed video recordings of the feeding behavior of free-swimming fish. High-speed video provides basic information that enables us to address the question, "How do tarpon capture their prey?" Second, information from this study can be incorporated in the formulation of fishing guidelines for anglers (Larmouth, personal communication). Third, because tarpon is considered an ancestral fish (Gosline 1971), this study will provide much needed information on prey-capture behavior and kinematics that will contribute to our understanding of the evolution of teleost feeding mechanisms, as well as the behavioral and ecological bases of the diversity of feeding systems in fishes (Lauder 1981; Richard and Wainwright 1995; Budick and O'Malley 2000).

The objectives of this study are twofold: (1) to describe the behavior of prey-capture in free-swimming tarpon and (2) to examine the kinematics of prey-capture in tarpon by quantifying the movements of key elements of the oral jaws and cranium while the fish captures its prey.

## METHODS

Juvenile tarpon were collected from the Indian River Lagoon, east-central Florida during summer 2000 using a 15 m × 1.5 m beach seine (mesh size = 5 mm). Within two hours of collection, fish were transported to the Florida Institute of Technology fish biology laboratories where each fish was kept in separate 38 l recirculating tanks for a period of two months. The fish were maintained in a controlled room at a salinity of 32-35 ppt, photoperiod of 12h L: 12h D, and temperature of 20-21°C. Tarpon were trained

to feed on live mosquitofish (*Gambusia affinis*) presented with forceps. Two 50 W halogen lights were turned on during feeding, in an attempt to maintain typical and consistent patterns of prey capture during filming. In order to minimize the confounding effect of prey size on feeding behavior and kinematics, prey size (i.e., maximum body diameter) was maintained at less than 50% of tarpon maximum gape (Werner 1974; Richard and Wainwright 1995). Live prey were introduced in mid-water based on our preliminary observations that tarpon did not attempt to capture prey introduced at the bottom of the tank and that prey introduced at mid-water swam toward the surface before being captured by tarpon.

Four juvenile tarpon (96.4 – 114.6 mm standard length) were filmed over a period of ten days using high-speed videography. We selected fish of similar size to avoid size-effects on kinematics (Richard and Wainwright 1995). Each fish was filmed while free swimming in a 50.5 cm × 30 cm × 25.5 cm (38 l) filming tank equipped with a 14 cm × 14 cm grid for scaling purposes. *G. affinis* was chosen as prey because it is an abundant poeciliid in the geographic location where the specimen were collected (Shenker, personal communication). Also, *G. affinis* was available in a wide range of sizes in correlation with the gape size of tarpon studied. Prey were introduced to the filming tank using forceps and released in the water column just in front of the reference grid. Each feeding event was recorded at 500 frames per second using a Redlake Imaging Motion Scope 2000-S monochrome high-speed digital video system (Redlake MASD, Inc, San Diego, California). A total of 20 feeding events were recorded for each fish. However, only feeding events that met the following criteria were included in the kinematic analyses: (1) the recorded sequence included the entire feeding repertoire (i.e., tarpon approaching prey, capturing prey, and moving away from prey capture site); (2) the tarpon swam perpendicular to the camera during feeding; and (3) all morphological structures used as reference points (e.g., tip of the oral jaws, posterior edge of the opercular bones) were clearly visible in the recorded images.

## Kinematic Analysis

A total of 20 recorded feeding events (five per fish) were analyzed using NIH Image (SCION Image Corp, Frederick, Maryland) and Redlake Imaging software (Redlake MASD, Inc, San Diego, California). Each feeding event was played back frame-by-frame and all measurements were repeated up to three times to increase precision; mean of repeated measurements was used in subsequent analyses. Six landmarks were digitized in each frame (see Figure 1). The positions of these landmarks were used to calculate 12 kinematic variables. The entire prey-capture kinematic event started at the frame preceding initial mouth opening and ended at the frame immediately following

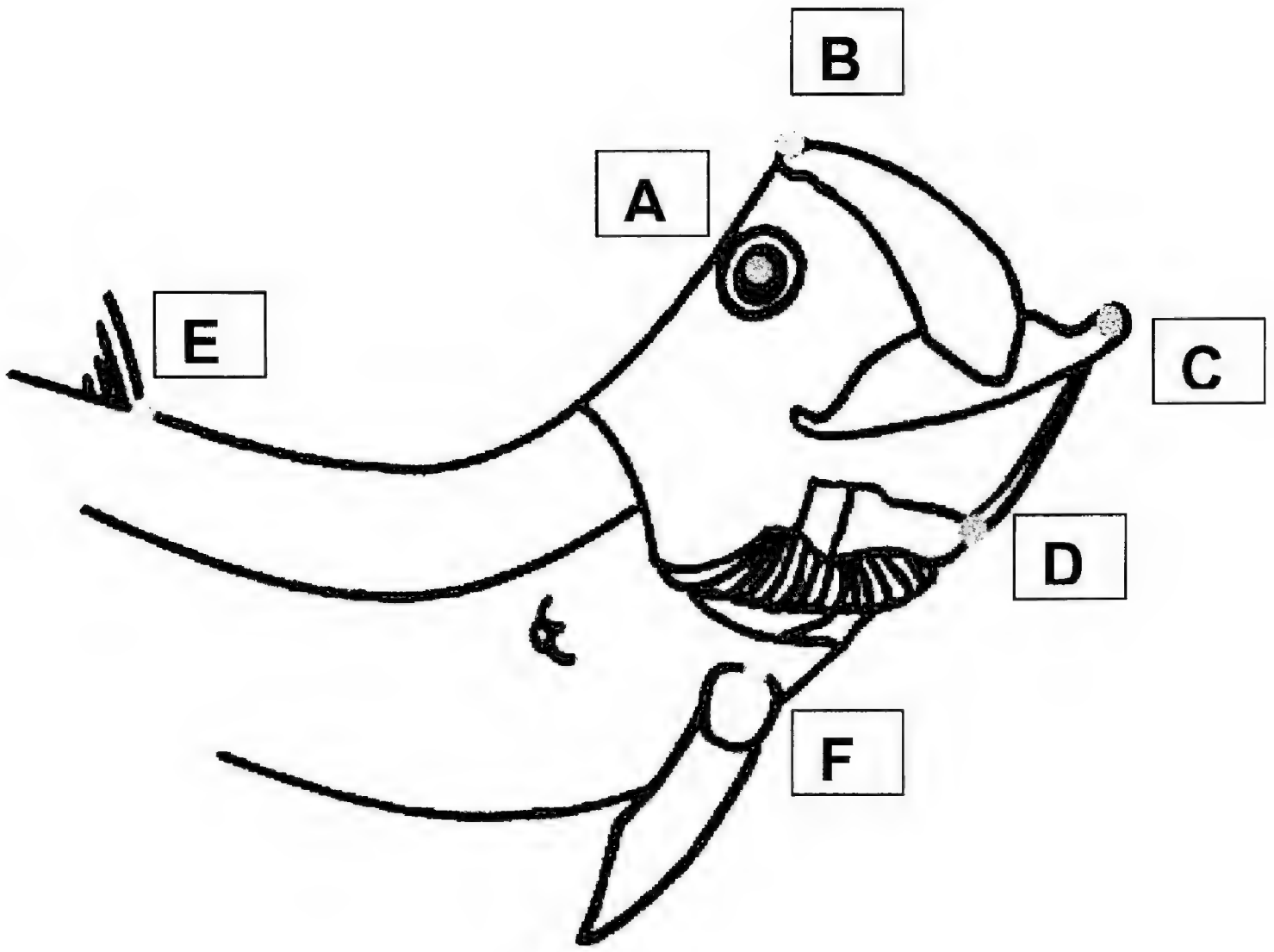


Figure 1. Schematic representation of the six anatomical landmarks on the juvenile tarpon used as reference points to generate 12 kinematics variables.
(A) Center of the eye, (B) tip of the maxilla, (C) tip of the dentary bone, (D) posterior end of the hyoid bone, (E) insertion point of the first dorsal spine, (F) mid-point of the base of the pectoral fin.

mouth closing. Kinematic variables were classified into three categories: (1) maximum excursions, (2) timing variables, and (3) velocities and acceleration.

Maximum Excursions

(1) Maximum gape was measured as the maximum distance from the tip of the maxilla to the tip of the dentary bones (Figure 1, B to C). (2) Maximum hyoid depression was measured as the maximum distance from the center of the eye to the anterior tip of the hyoid bone (Figure 1, A to D). (3) Maximum head elevation was measured as the angle between the line connecting the base of the first dorsal fin spine to the tip of the maxilla and the line connecting the base of the first dorsal fin spine to the mid-point of the base of the pectoral fin (Figure 1, B, F, to E).

Timing Variables

(1) Duration of the prey-capture cycle was the time from initial mouth opening to mouth closing. (2) Time to maximum gape was the time from initial mouth opening to maximum gape. (3) Time to maximum hyoid depression was the time from initial mouth

opening to maximum hyoid depression. (4) Time to maximum head rotation was the time from initial mouth opening to maximum head rotation.

### Velocity and Acceleration

(1) Approach velocity was defined as the ratio of the distance traveled by the tarpon (using the center of the eye as a reference point) and the time elapsed from the first approach toward the prey to initial mouth opening. (2) Lunge velocity was defined as the ratio of the distance traveled by the tarpon (using the mid-point of the base of the pectoral fin as reference point) and the time elapsed from initial mouth opening to maximum gape. The base of the pectoral fin was chosen as a reference point and not the center of the eye because of the tremendous head rotation observed during a prey-capture event. (3) Attack acceleration was the ratio of the difference between lunge velocity and approach velocity divided by the time elapsed from time of initial approach to time of maximum gape. (4) Head rotation velocity was the ratio of the angular displacement and time elapsed from initial to maximum head rotation.

## RESULTS

### Feeding Behavior

During all recording sessions, tarpon fed aggressively. Prey was always approached from underneath, captured with the oral jaws, and swallowed whole (Figure 2). Vigorous forward motion of the fish appeared to facilitate transport of the prey from the mouth to the pharyngeal apparatus, then to the esophageal opening. Tarpon approached each prey slowly (mean approach velocity = 197.7 mm/s ± 27.4, Mean ± S.E.M.), swimming slightly below the prey. When the prey was within striking distance (mean distance between prey and tip of tarpon's mouth = 19.0 mm ± 1.2), an explosive prey capture event was initiated by sudden acceleration at a rate of 3.7 $m/s^2$ ± 0.7 in order to reach a lunging speed of 355.7 mm/s ± 40.4 towards the prey. A peculiar flaring of the opercular bones was observed in tarpon immediately after prey was captured. The prey-capture event ended with the prey fully engulfed in the oral cavity as the tarpon slowly swam away from the capture site, toward the bottom of tank, while prey was being swallowed. On average, a prey capture cycle lasted 159.4 ms ± 12.1.

### Kinematics of Prey Capture

The kinematic profile of a typical prey-capture cycle is presented in Figure 3. Two primary features of this kinematic profile are observed. First, there is a rapid increase in excursions of gape, hyoid, and head rotation to open the mouth until maximum gape is achieved. This phase represents roughly the first third of the prey-capture cycle. Second,

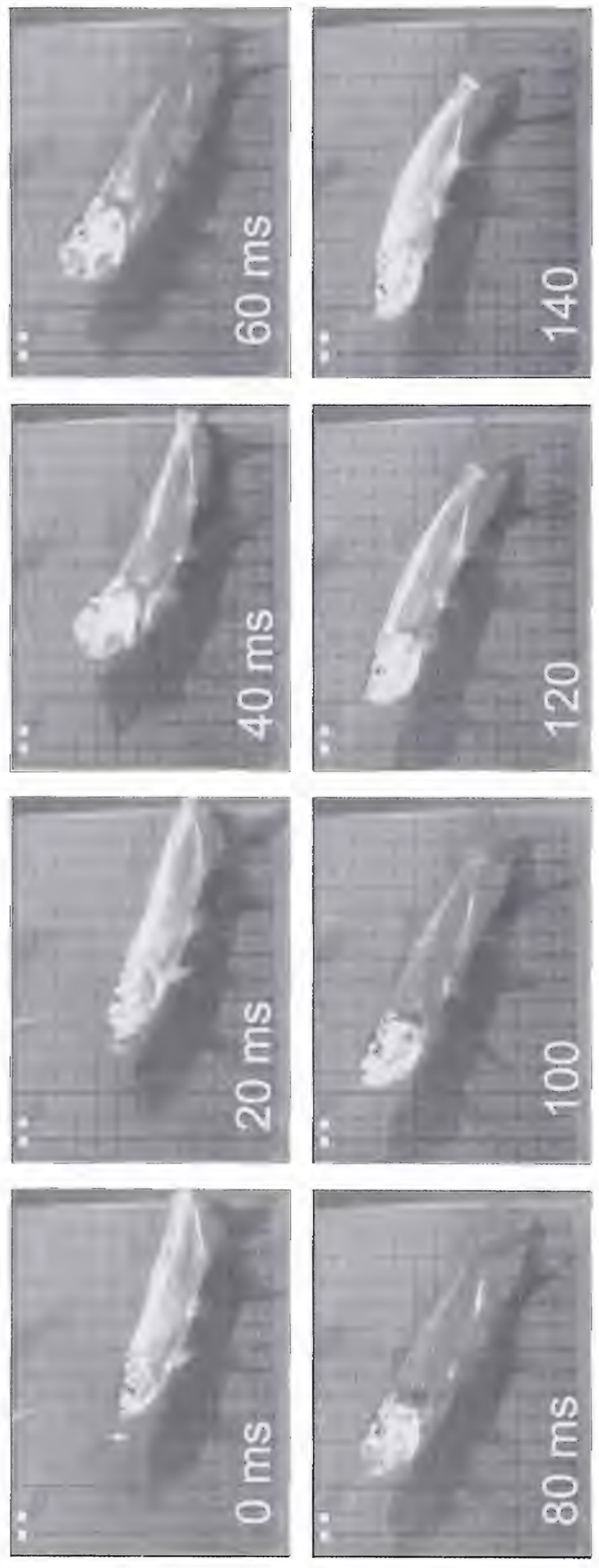


Figure 2. A set of eight video fields showing a representative profile of prey capture behavior in juvenile tarpon, *Megalops atlanticus*. The filming rate was 500 frames per second at a shutter speed 1/1000 second. Successive frames are 20 ms apart. Maximum gape was reached 40 ms after initial mouth opening (0 ms). The duration of prey capture cycle lasted for 140 ms.

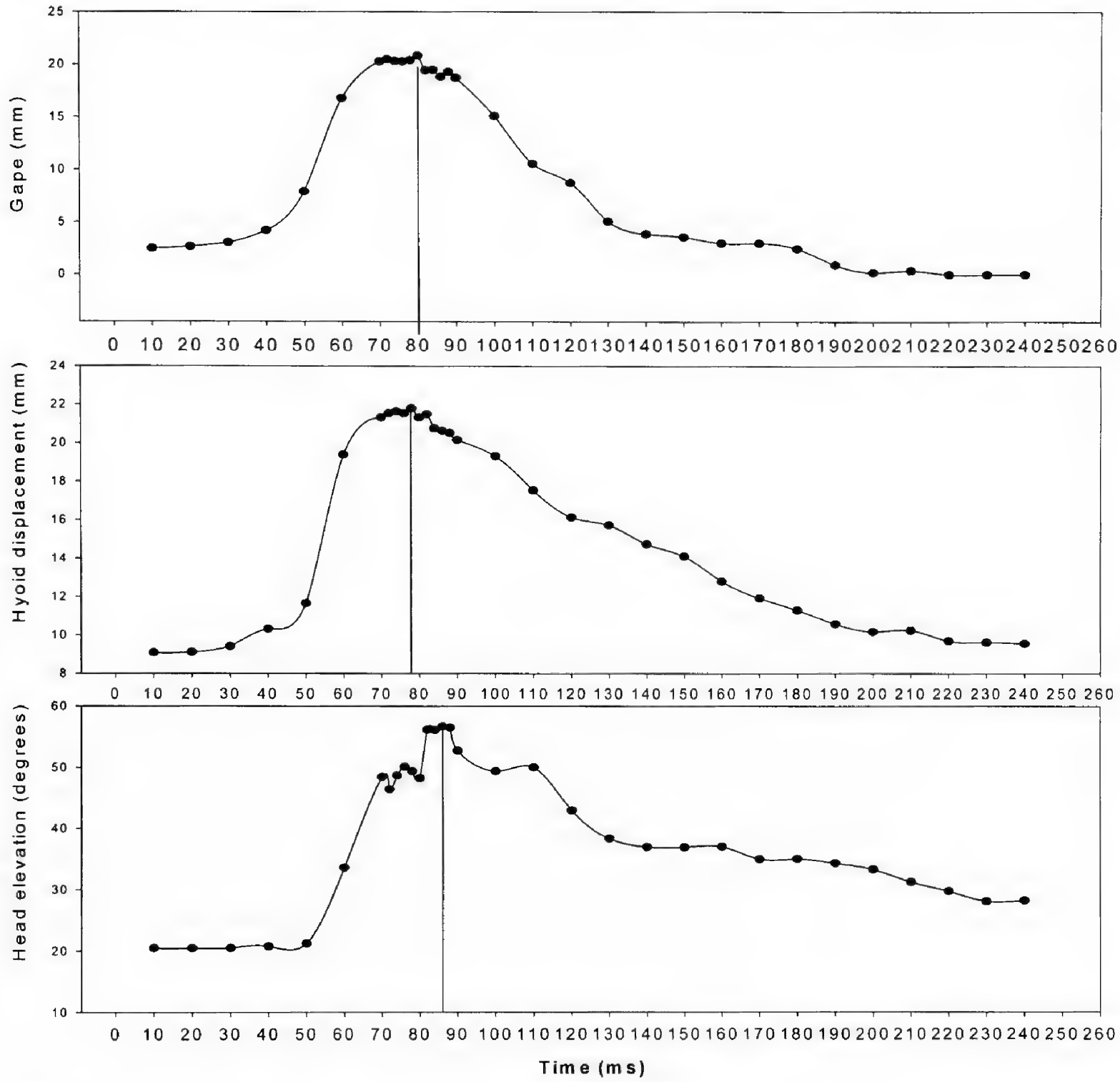


Figure 3. Representative kinematic profiles of gape, hyoid, and head displacement during prey capture in tarpon. Note that none of the three profiles are symmetrical along the time axis. These profiles indicate that the velocity of buccal expansion and jaw opening is much faster than the velocity of buccal compression and jaw closing.

following maximum excursions of these key kinematic features, there is a slower rate of decreasing kinematic displacement to close the mouth, as the jaws, hyoid and other cranial elements return to pre-strike positions.

Table 1 presents the descriptive statistics for the 12 kinematic variables measured in this study. Three kinematic events appeared to drive the prey-capture behavior in tarpon. First, the main component of the prey-capture attack was the rapid, postero-dorsal rotation of the head (mean angular velocity of head rotation = 713.1 degree per second ± 104.6). On average, head rotation always started before maximum gape was achieved

Table 1. Mean ± Standard Error (S.E.) of kinematic variables measured during prey capture behavior in *Megalops atlanticus*. All timing variables, except time to maximum gape, were standardized with time to maximum gape being equal to zero for convenient representation of the timing profile. A negative value indicates that the kinematic event preceded maximum gape. Time to maximum gape itself was represented by the time lapse from initial mouth opening to maximum gape.

| Kinematic variables | Fish 1 (111.7 mm SL) | Fish 2 (114.6 mm SL) | Fish 3 (100.1 mm SL) | Fish 4 (96.4 mm SL) | Overall Mean (all 4 Fish) |
|---|---|---|---|---|---|
| Duration of feeding cycle (ms) | 142.8 ± 8.4 | 186.4 ± 26.4 | 172.8 ± 26.0 | 135.6 ± 11.8 | 159.40 ± 12.1 |
| Maximum gape (mm) | 21.7 ± 0.4 | 21.0 ± 0.5 | 19.8 ± 0.3 | 18.7 ± 0.6 | 20.3 ± 0.7 |
| Time to maximum gape (ms) | 51.2 ± 6.6 | 62.8 ± 10.9 | 50.4 ± 4.7 | 54.8 ± 15.4 | 54.8 ± 2.8 |
| Time to initial cranial rotation (ms) | -22.4 ± 0.7 | -15.6 ± 1.5 | -17.2 ± 1.0 | -14.0 ± 1.4 | -17.3 ± 1.8 |
| Maximum cranial rotation (mm) | 48.0 ± 2.0 | 55.8 ± 1.3 | 49.1 ± 0.9 | 52.2 ± 1.9 | 51.3 ± 1.7 |
| Time to maximum cranial rotation (ms) | 2.0 ± 1.8 | 4.4 ± 1.6 | 2.0 ± 1.3 | 2.8 ± 0.5 | 2.8 ± 0.6 |
| Maximum hyoid depression (mm) | 21.7 ± 0.7 | 23.5 ± 0.4 | 21.2 ± 0.3 | 20.1 ±0.7 | 21.6 ± 0.7 |
| Time to maximum hyoid depression (ms) | 4.8 ± 5.9 | 2.4 ± 1.3 | 1.2 ± 1.9 | -2.0 ± 4.6 | 1.6 ± 1.4 |
| Angular velocity of cranial rotation (°/s) | 434.6 ± 55.7 | 931.2 ± 75.9 | 697.2 ± 77.5 | 789.6 ± 47.6 | 713.1 ± 104.6 |
| Approach velocity (mm/s) | 266.0 ± 29.0 | 208.0 ± 21.1 | 182.6 ± 43.1 | 134.2 ± 28.3 | 197.7 ± 27.4 |
| Lunge velocity (mm/s) | 404.0 ± 41.4 | 328.6 ± 30.2 | 435.4 ± 25.0 | 255.0 ± 57.2 | 355.7 ± 40.4 |
| Acceleration ($m/s^2$) | 3.1 ± 1.0 | 2.1 ± 0.7 | 5.5 ± 1.4 | 4.2 ± 2.5 | 3.7 ± 0.7 |

SL = Standard length, n = 5 for each fish.

(mean onset of head rotation relative to maximum gape = -17.3 ms ± 1.8). In addition, in all cases, maximum head rotation occurred after maximum gape was achieved (mean time to maximum head rotation relative to time of maximum gape = + 2.8 ms ± 0.6). Second, the time to maximum hyoid depression was more variable, occurring either

before or after maximum gape was achieved (mean time to maximum hyoid depression relative to time to maximum gape = 1.6 ms ± 1.4). Third, from an average approach velocity of 197.7 mm/s ± 27.4 the tarpon accelerated at an average of 3.7m/s$^2$ ± 0.7 to an average lunging velocity of 355.7 mm/s ± 40.3 to engulf its prey.

## DISCUSSION

The prey-capture behavior of *M. atlanticus* appears to be unique compared to teleost fishes that have been shown to capture their prey whole by either suction feeding or ram feeding. The feeding repertoire of tarpon involves swimming to approach the prey from underneath, accelerating at a short distance toward the prey, rotating its head, depressing its hyoid, opening its mouth to engulf the prey, and then swimming in the opposite direction to swallow the prey. In suction-feeding teleosts, fishes approach their prey and draw water and prey into the mouth by creating sub-ambient pressure in the buccal cavity during the expansive phase of the prey-capture cycle until maximum gape is achieved (Lauder 1981). Fish that capture prey by ram feeding open their mouth while approaching the prey and subsequently engulf the prey using the momentum created by accelerating forward (Norton and Brainerd 1993). The kinematics of a prey-capture cycle in tarpon is characterized by two major events: (1) a rapid expansive phase involving postero-dorsal cranial rotation, hyoid depression, and mouth opening that occurs during the first third of the cycle as the prey is being captured and (2) a slower compressive phase involving antero-ventral rotation of the head, hyoid elevation and closing the mouth to swallow prey.

Previous studies on teleost feeding behavior showed that the kinematic displacement profiles typically follow a symmetrical, "bell shape" curve (Richard and Wainwright 1995; Gibb 1995; Westneat and Wainwright 1989), indicating that the duration of the expansive phase is similar to that of the compressive phase of the prey-capture cycle. In contrast, this study demonstrates that tarpon exhibit an asymmetrical kinematic pattern of prey-capture (Figure 3). This indicates that the expansive phase of the prey-capture cycle (i.e., buccal expansion and oral jaw opening to capture prey) occurs more swiftly at the initiation of the strike than the compressive phase (i.e., jaw closing and return of cranial elements to pre-strike conditions). We provide three plausible explanations for the asymmetrical kinematic profile of prey capture in tarpon. First, our examination of the functional morphology of the feeding mechanism in tarpon indicated that the muscles involved in closing the mouth are less massive than those of the jaw opening muscles. Perhaps closing of the mouth involves a slower, passive "recoil" of the expanded buccal cavity. In suction feeding fishes that exhibit a similar duration in the expansive and compressive phases of the feeding event, the adductor mandibulae complex (i.e., the main jaw-closing musculature) is relatively more massive than the condition found in tarpon

(e.g., Turingan and Wainwright 1993; Richard and Wainwright 1995). Closing of the mouth in the latter fishes involve a more active firing of the adductor mandibulae muscles in contrast to the slower, passive "recoil" that we propose for tarpon. Second, the tarpon continues its forward motion with the mouth still open, thus further reducing the speed of mouth closing. Third, forward movement with the mouth open may initiate prey transport into the esophagus.

The basic kinematic profile and the associated feeding repertoire in tarpon that we describe in this study provide much needed information on relatively less derived fish taxa. Over the past two decades, kinematic and electromyographic data have been used to construct phylogenetic hypotheses in an attempt to explain the evolution of the diverse feeding mechanisms in fishes (Chu 1989; Westneat 1990; Gibb 1995; Grubich 2000). However, with the exception of the detailed work of Lauder (1980) that described the evolution of the feeding mechanism in primitive actinopterygian fishes, much of the work on feeding kinematics and electromyography focused on the relatively more derived Percomorpha (Westneat and Wainwright 1989; Norton and Brainerd 1993; Gillis and Lauder 1995; Wainwright and Shaw 1999). We provide feeding kinematics and behavioral information on a primitive Teleostei (*Megalops atlanticus*; Elopomorpha, Nelson 1994) that are useful in understanding evolutionary transitions leading to the well known percomorph feeding mechanism.

The extent to which our basic study on the feeding kinematics and behavior benefits the avid fly or hook and line fisherman may be extensive, but we can only offer a few here. First, the tarpon always strikes as the prey moves above it, thus the use of surface lures or flies is usually successful. Second, the tarpon approaches its prey slowly; any disturbance during this approach startles the predator and will halt prey capture attempts. Thus as soon as the live bait or lure hits the water, a slow, smooth reeling is recommended. Third, the use of a fast moving bait is not recommended because our study demonstrated that the tarpon is not attracted to very elusive prey. Finally, our observation that the tarpon closes its mouth more slowly after prey is captured leads us to recommend that the angler sets the hook a second or two after feeling that the tarpon has hit the bait.

The extent to which tarpon modulate their feeding behavior and kinematics remains to be explored. Fishes are known to vary their prey-capture behavior depending on the behavior of prey (Sanderson 1990; Nemeth 1997), hardness and elusiveness of prey (Turingan and Wainwright 1993), and prey size (Ferry-Graham 1998a). The kinematics of prey-capture also changes throughout ontogeny in fishes (Richard and Wainwright 1995; Ferry-Graham 1998b; Wainwright and Shaw 1999; Hernandez 2000). Our ongoing research investigates prey type-induced versatility and scaling of feeding kinematics during ontogeny in tarpon. These themes are important because we still lack an

understanding of the behavioral and physiological changes that tarpon undergo as they migrate from nursery grounds (estuarine and shallow coastal waters) to their adult habitats (deeper coastal and open waters).

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# RECRUITMENT OF TARPON (*MEGALOPS ATLANTICUS*) LEPTOCEPHALI INTO THE INDIAN RIVER LAGOON, FLORIDA

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## ABSTRACT

The movement of larval tarpon (*Megalops atlanticus)* from the Atlantic Ocean into the nursery grounds of the Indian River Lagoon, Florida was monitored during the summers of 1994 and 1995 by four channel nets moored at the surface of Sebastian Inlet. A total of 253 and 723 tarpon leptocephali (13-26 mm SL) were collected during 1994 and 1995, respectively. Catches in both years showed significant lunar cycles, with peak recruitment occurring 2-4 days prior to summer full moon periods. Dramatic variability was observed in the magnitude of recruitment during each lunar cycle. During 1994, most recruitment occurred during a 10-day long pulse in July, with smaller pulses in June and August. No direct associations with environmental events were detected. During 1995, short recruitment pulses occurred in June, but recruitment was almost non-existent in July. Passage of Hurricane Erin directly over the study site at the beginning of August was followed by greater recruitment in a 5-day period than was found throughout the rest of the entire 2-year study. Sagittal otoliths were removed from 93 randomly-selected specimens collected in 1994, embedded and examined with a Scanning Electron Microsope. Based on the assumption that increments observed in the otoliths were deposited on a daily basis, larvae had a mean age of 20.2 days (range = 15-26 days). Back-calculation of hatching dates indicates that these larvae were spawned around the full moon periods in May, June and July.

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## INTRODUCTION

Tarpon (*Megalops atlanticus*) are a highly prized target of sportfishing enthusiasts in Atlantic tropical, subtropical and temperate waters from Virginia to Brazil, including the Gulf of Mexico and the Bahamas, as well as tropical west Africa (Wade 1962; Smith 1980; Zale and Merrifield 1989; Nelson 1994). Despite tremendous recreational interest in *M. atlanticus*, little is known regarding the factors that affect the population dynamics of this valuable gamefish.

Initial studies on the reproductive biology suggested that *M. atlanticus* spawn around nearshore reefs and estuarine inlets (Breder 1944; Wade 1962). Subsequent research, however, indicated that fish migrate and spawn in offshore waters. Although precise spawning sites have not yet been identified, Smith (1980) reported on the capture of 5.8-22.3 mm leptocephalus larvae in surface waters beyond the 200 m isobath from the southwest Gulf of Mexico, off Cozumel, and southwestern Florida. On the west coast of Florida, *M. atlanticus* aggregate inshore during the late spring and summer prior to migrating into the Gulf of Mexico (Crabtree 1995; Crabtree et al. 1992, 1997). The smallest (5.5 mm) larvae collected by Crabtree et al (1992) over the continental slope, 250 km west of Florida, had an otolith-estimated age of 2 days. Spawning apparently occurs along the southeast coast of the United States as well, with 6.5-21.5 mm larvae being collected off North Carolina (Berriens et al. 1978).

Although some aspects of the biology of *M. atlanticus* leptocephali have been described, including development, morphology, and physiology (Wade 1962; Eldred 1967; Smith 1980, 1989; Cyr 1991; Crabtree et al. 1992), little is known about the patterns and mechanisms of onshore movement toward the estuarine systems that have been identified as nursery habitats (Breder 1944; Rickards 1968; Gilmore 1977, Gilmore and Herrema 1981, Zale and Merrifield 1989). Shenker et al. (1995) determined that larval *M. atlanticus* could be captured in channel nets as they moved from the pelagic larval habitat into an estuarine nursery. The primary objective of the present study was to build on the preliminary study of Shenker et al. (1995), and intensively characterize the recruitment of *M. atlanticus* larvae into an estuarine ecosystem.

In this study, we used moored channel nets during two consecutive summers to characterize temporal and spatial patterns of larval entry through an inlet between the Atlantic Ocean and the Indian River Lagoon. Concurrent environmental data were collected to examine possible mechanisms that influence recruitment events. Otoliths of larvae were examined to determine their age at recruitment into the IRL, and to calculate their hatching dates.

## MATERIALS AND METHODS

### Study Site

The Indian River Lagoon ecosystem (Figure 1) is a shallow, narrow estuarine system located between barrier islands and the Florida mainland. It hosts a diverse assemblage of warm temperate and tropical Caribbean ichthyofauna (Gilmore 1977; Gilmore and Herrema 1981). Sampling was conducted at Sebastian Inlet, one of five inlets connecting the IRL with the Atlantic Ocean. The man-made inlet, constructed in 1886, is periodically dredged to maintain flow. The outer edge of the continental shelf, 40 km east of the inlet, is swept by Gulf Stream water flowing to the north. Alongshore currents between the coast and the northward-flowing Gulf Stream tend to oscillate in response to meteorological conditions (Pomeroy et al. 1993).

### Larval and Environmental Data

*Megalops atlanticus* leptocephali were collected from the Sebastian Inlet during the summers of 1994 (25 May -12 September) and 1995 (8 June-2 September) using four channel nets moored approximately 10 m from the edges of the north and south navigation channels (Figure 2). Nets fished the upper meter of water in the approximately

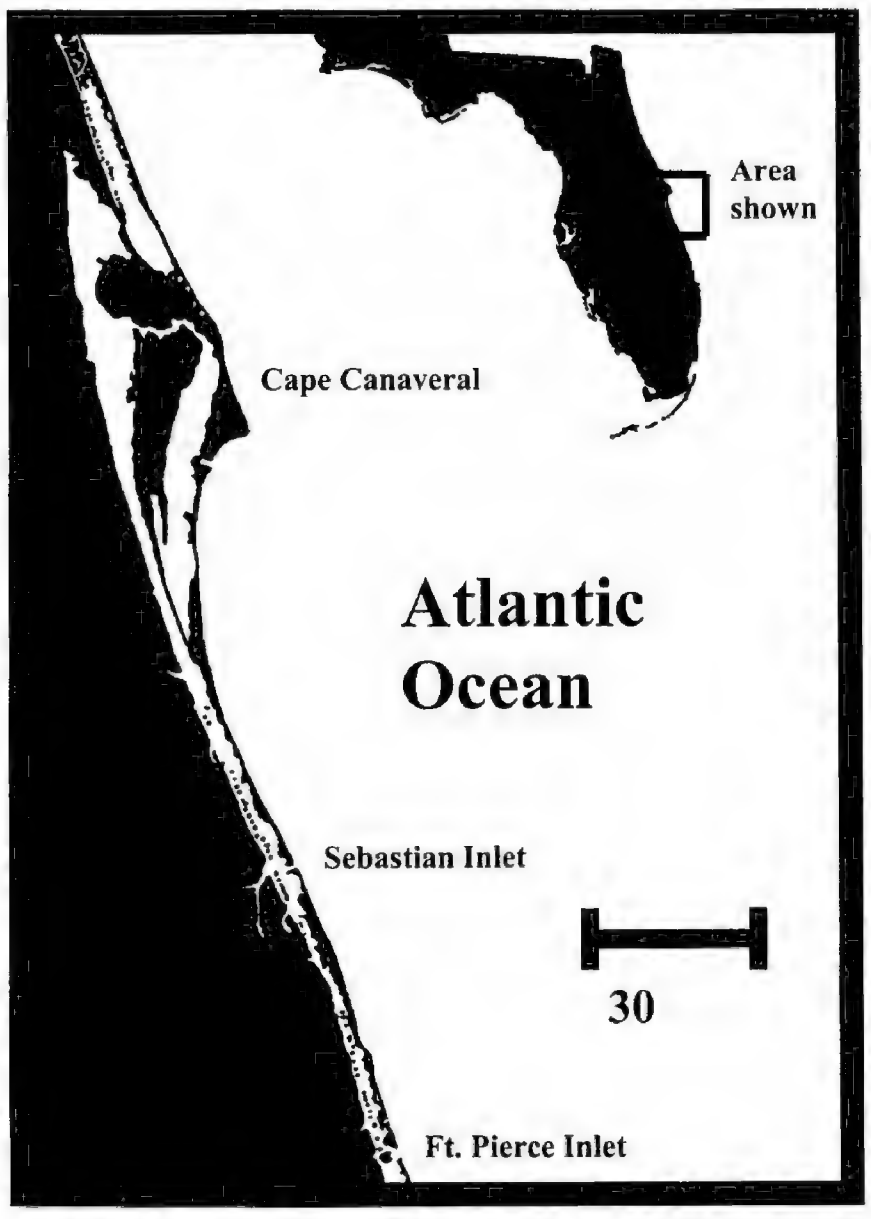


Figure 1. Location of Sebastian Inlet and the Indian River Lagoon, Florida

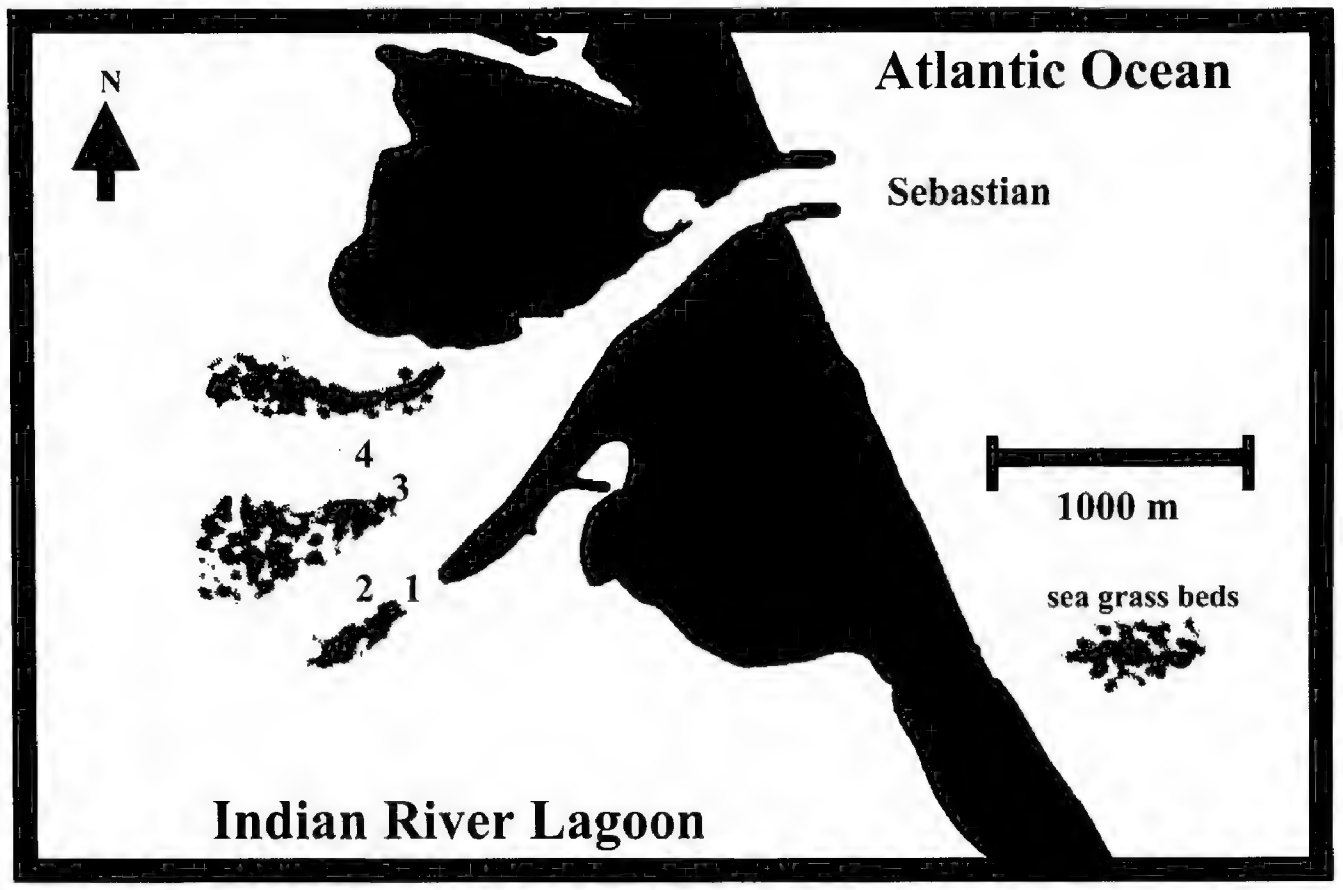


Figure 2. Site of channel net stations (1-4) in Sebastian Inlet, Florida

2 m deep southern channel (Stations 1 and 2) and the 3 m deep northern channel (Stations 3 and 4). Preliminary sampling during 1993 with nets fixed to a frame and anchored at the bottom of the northern channel indicated that little, if any, larval transport occurred along the bottom layer of the inlet (Shenker, unpubl. data). Nets were based on the design of Shenker et al. (1993), with a mesh of 1.2 mm, and a mouth area 1.5 m wide by 1.0 m deep. Because these nets rotated with the changing tides, both flood and ebb tide samples were collected during each 24 hour sampling period. The negatively-buoyant cod ends pinched the nets closed during low current periods, preventing fish from escaping during tide changes. Our data analysis assumes that *M. atlanticus* leptocephali moved through the inlet only during night-time flood tides, as observed during discrete flood and ebb tide sampling conducted in 1993 (Shenker, unpubl. data).

Samples were removed daily from each net between 09:00 and 10:00 hrs. Macroalgae and flotsam were immediately removed from the sample, and leptocephalus larvae were preserved in 70% ethanol for later identification and otolith analysis. Leptocephali were identified to species according to dorsal and anal fin position and myomere counts (Smith 1989). Measurement of 20 larvae upon capture, and after 7 days of preservation, was used to determine the shrinkage effect of the preservative. The mean correction factor of 9% was used to calculate the live SL of ethanol-preserved *M. atlanticus*. Other fish larvae were preserved in 10% formalin for examination of other taxa. Nets were scrubbed daily to remove debris from the mesh, and were rotated every few days with nets that had been completely cleaned with a pressure-washer and dried on the dock.

A weather station located at the Sebastian Inlet State Park ranger station collected hourly rain, wind, temperature and barometric pressure data throughout the study period. Wind data were averaged over 24 hour periods to generate daily wind data.

## Otolith Analysis

Larvae collected during 1994 were transferred to the Florida Marine Research Institute, St. Petersburg, for preparation. A subsample of 93 randomly-selected larvae were prepared for otolith analysis by embedding the heads in high density resin and sectioning to the cores of the sagittal otoliths, following the methodology of Haake et al. (1982). Otoliths were then prepared for etching for Scanning Electron Micrograph (SEM) analysis with 0.05% HCl at room temperature for 5-60 sec. SEM images were returned to the Florida Institute of Technology for reading.

Utiliziling the assumption that otolith increments were deposited on a daily basis (Crabtree 1995), we evaluated the age of each larva by counting increments on each otolith. Two readers independently evaluated each SEM photograph twice, and without knowledge of previous counts. If the four independent counts varied more than $\pm$ 3, the otolith was eliminated from the subsequent analysis.

## Data Analysis

To generate a nightly index of larval recruitment, catches of all four channel nets were summed for each night during the summers of 1994 and 1995. To test for possible associations between meteorological conditions and nightly recruitment, mean daily wind data were divided into onshore/offshore and alongshore components of motion. The proportions of total *M. atlanticus* recruitment occurring under each of the wind conditions were compared with the frequency that each wind condition occurred (G-test; Sokal and Rholf 1981).

To evaluate potential lunar periodicity in larval entry into the IRL, circular analysis (Batschelet 1981; Zar 1984) was used. Data from three complete lunar cycles for each of 1994 and 1995 were combined into one lunar month. The number of recruits were summed for each lunar night, and plotted to examine the modality of recruitment patterns throughout the lunar cycle. The mean night of the lunar recruitment for each taxon was determined by calculating the mean rectangular coordinates:

$$X=f_i\cos(a_i\backslash n) \text{ and } Y=f_i\sin(a_i/n)$$

where $f_i$ = proportional frequency of recruits on each night, n = number of lunar nights, and $a_i$= midpoint of the angle interval ($360^o/29.4$) (Zar 1984). A correction factor was applied to account for any bias in the computations due to the grouped data:

$$c=d/360^o\backslash\sin(d/2)$$

where d = degree interval (= 29.4 days) (Zar 1984). The nonparametric Rayleigh test was used to test the null hypothesis that recruitment was uniformly distributed around the

lunar month (i.e., there was no mean direction in the circular distribution; Batschelet 1981; Zar 1984).

A circular analysis and the Rayleigh test were also used to examine possible lunar periodicity in the otolith-estimated hatching dates of larvae collected in 1994.

## RESULTS

### Larval Recruitment

A total of 976 *M. atlanticus* leptocephali were taken during the two summers, with 74% of the recruitment occurring in summer 1995. Station 1, on the shallow southern side of the inlet, consistently collected the greatest numbers of leptocephali in both years (Figure 3). The deepest site, with the highest current velocity (Station 4) consistently produced the lowest catch rates during both years.

Leptocephalus recruitment was dominated by short pulses of onshore movement during both summers. In 1994, 73% of the total catch was obtained during a 13-night period in mid-July, with lesser pulses in early June and mid August (Figure 4). Winds typically blew southward during the summer (Figure 5), and no associations between recruitment pulses and specific meteorological events were evident. The major recruitment pulse observed in July occurred during a period when there were very light cross-shelf on-shore winds.

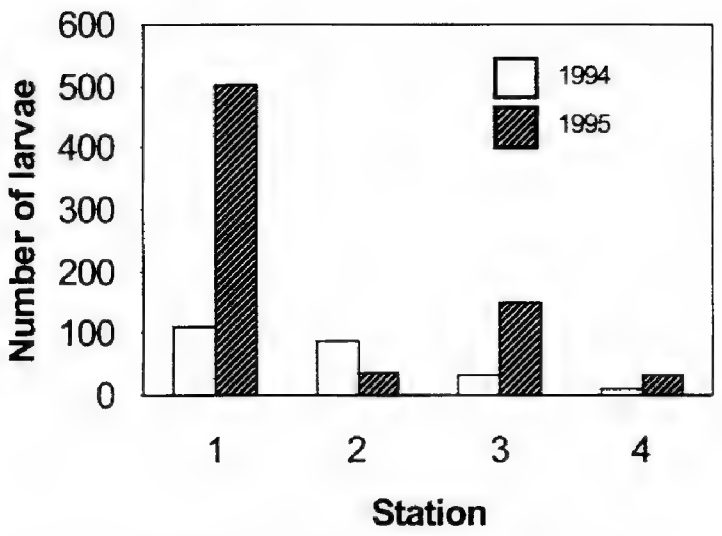


Figure 3. Total catches of larval *M. atlanticus* made at each of the channel net stations in Sebastian Inlet, Florida, during summer 1994 and 1995.

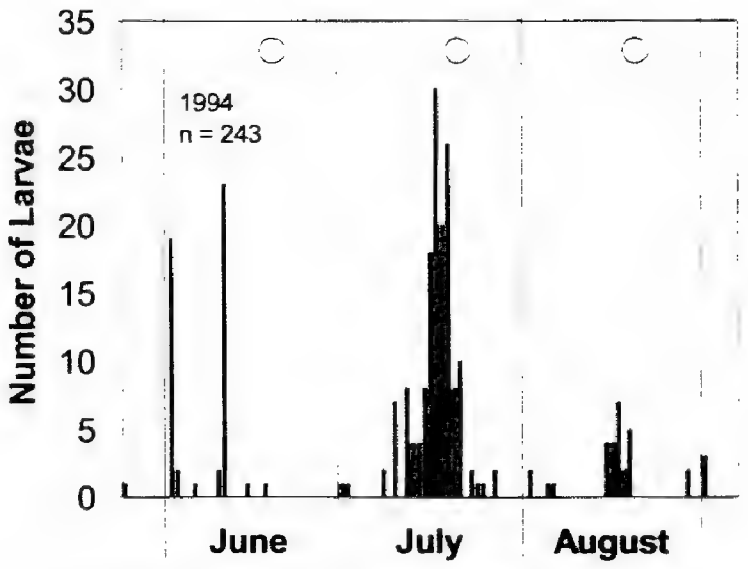


Figure 4. Daily catches of larval *M. atlanticus* captured at channel net stations in Sebastian Inlet, Florida, summer 1994. Open circles = full moons.

Despite the lack of association between recruitment and oceanographic or meteorological events, timing of the pulses suggested a lunar periodicity in recruitment. Circular statistical analysis (Rayleigh test, $z=529.1$, $p<0.05$) indicated that most

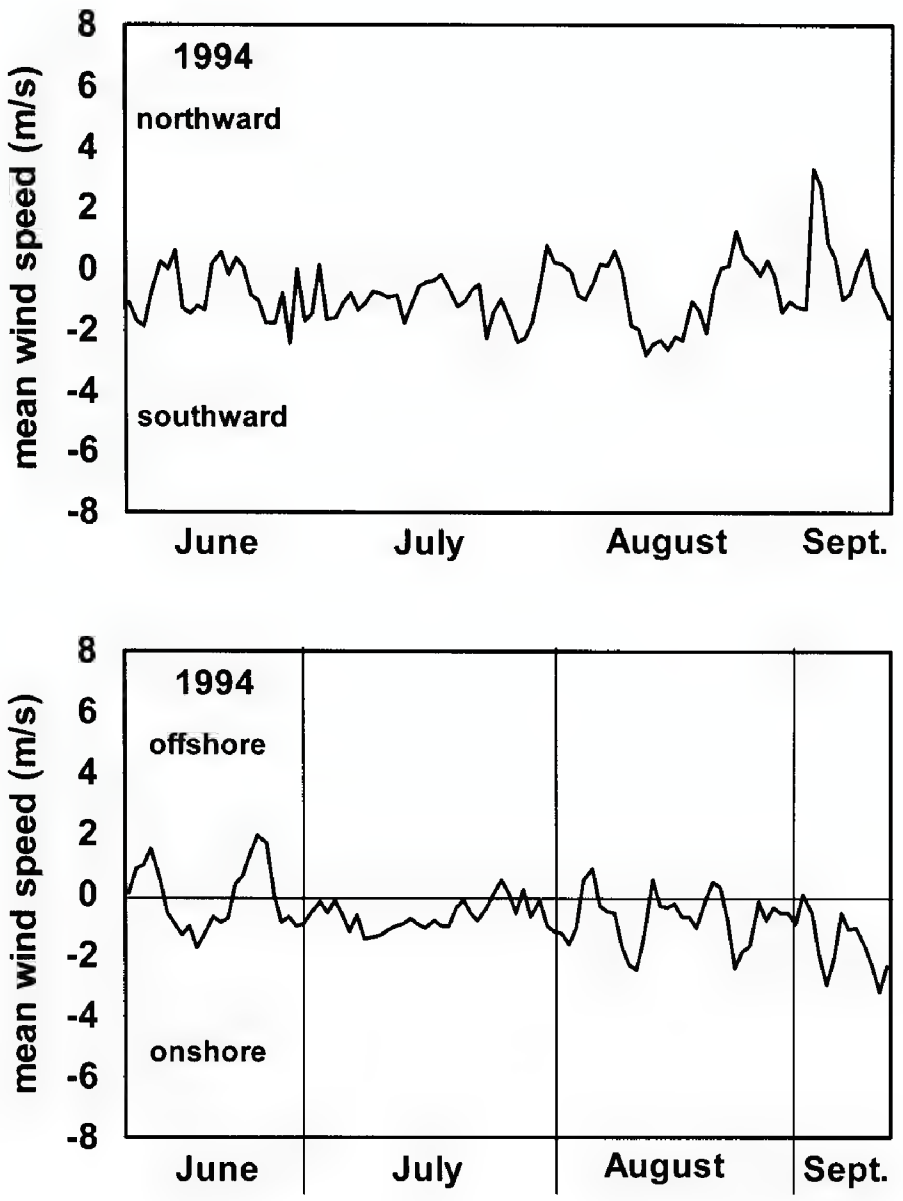


Figure 5. Cross-shelf and along-shelf components of wind at Sebastian Inlet, Florida, summer 1994.

recruitment occurred during the waxing moon phase (Figure 6) with peak catches made on lunar nights 11-13 (full moon = lunar night 15).

Recruitment of *M. atlanticus* leptocephali followed a very different pattern in 1995. Two short recruitment pulses occurred in June, resulting in capture of 172 larvae (Figure 7). Mean daily winds during these pulses were generally weak, with southward and onshore components of motion (Figure 8). Very minimal recruitment was then observed until 29 July, and nearly 50 leptocephali were collected on the night of 30-31 July. Sampling was then suspended for four days as Hurricane Erin moved onshore. The eye of this Category 1 hurricane passed directly over the sampling site shortly after midnight on 1 August. During the 5 days after resumption of sampling, 491 leptocephali (70% of the total catch for 1995) were collected (Figure 7). As in 1994, recruitment was not uniformly distributed within the lunar month (Rayleigh test, $z=8983.0$, $p<0.05$). Mean onshore movement of *M. atlanticus* occurred on lunar night 13, two nights prior to the full moon (Figure 9).

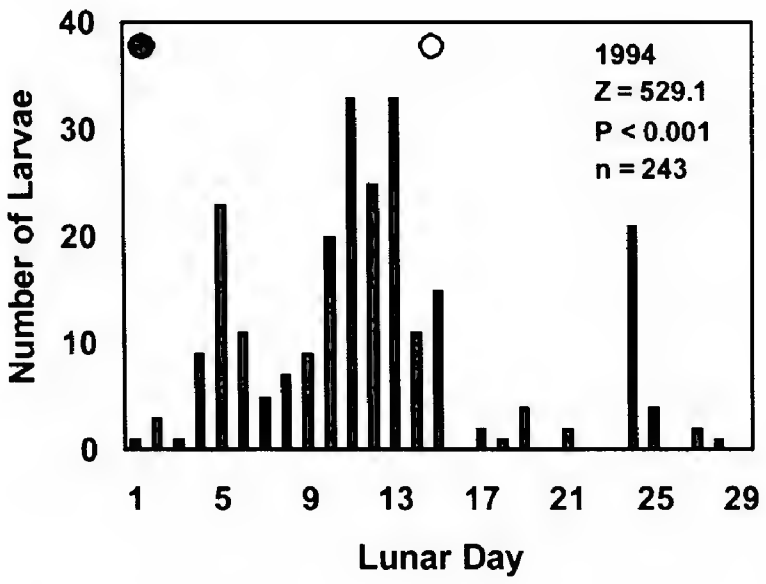


Figure 6. Lunar cycle of larval *M. atlanticus* catches made in Sebastian Inlet, Florida, during summer 1994. Rayleigh's test of circular distributions (Z= 529.1, P<0.001) indicates a non-uniform hatching distribution throughout the lunar months. Closed circle = new moon; open circle = full moon.

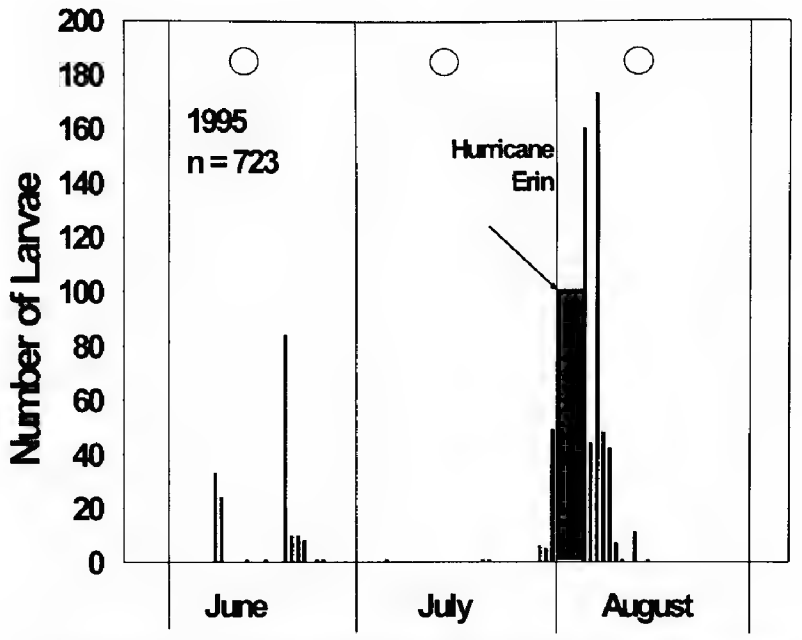


Figure 7. Daily catches of larval *M. atlanticus* captured at channel net stations in Sebastian Inlet, Florida, summer 1995. Open circles = full moons.

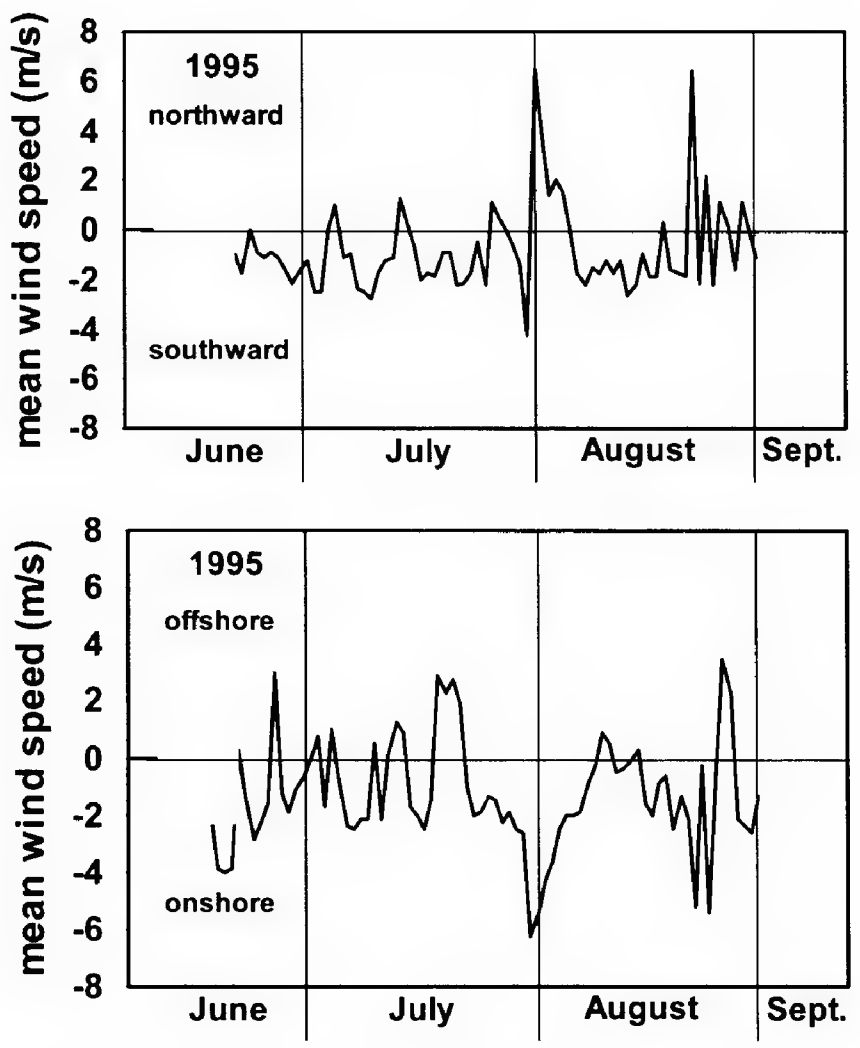


Figure 8. Cross-shelf and along-shelf components of wind at Sebastian Inlet, Florida, summer 1995.

## Larval Age and Size

Of the 93 larvae examined from the 1994 collection, a total of 41 possessed readable otoliths (Figure 10). Larvae ranged in age from 15-26 days, with a mean age of 20.2 days (Figure 11) and in size from 15.5-22.1 mm SL . There was no correlation between size and age (Figure 12), reflecting the tendency of leptocephali to grow during the larval stage, then shrink during metamorphosis. The timing of metamorphosis does not appear to be consistent in this species. The oldest larvae, with estimated ages of 24-26 days included the smallest fish (< 15 mm SL) as well as some of the largest (> 20 mm SL).

## Hatching Dates

Back-calculation of the hatching dates of the 41 otolith-aged larvae collected in 1994 indicates that these fish hatched from mid May to mid August (Figure 13). Hatching dates exhibited a significant lunar periodicity (Rayleigh's test (Zar 1984); Z = 11.71; P<0.001, n=41), with 71% of the larvae hatching within 10 days after the summer full moon dates (Figure 14). The dominant recruitment peak, occurring shortly before the full moon in July was associated with hatching around the full moon in June.

## Extension of Spawning Season

Analysis of otoliths of larvae caught in channel nets in Sebastian Inlet in 1994 generate estimates of a May-August spawning season that corresponds closely with Crabtree's (1995) analysis of leptocephali captured off the west coast of Florida. An additional study conducted in Sebastian Inlet in 1998, however, indicates that the tarpon spawning

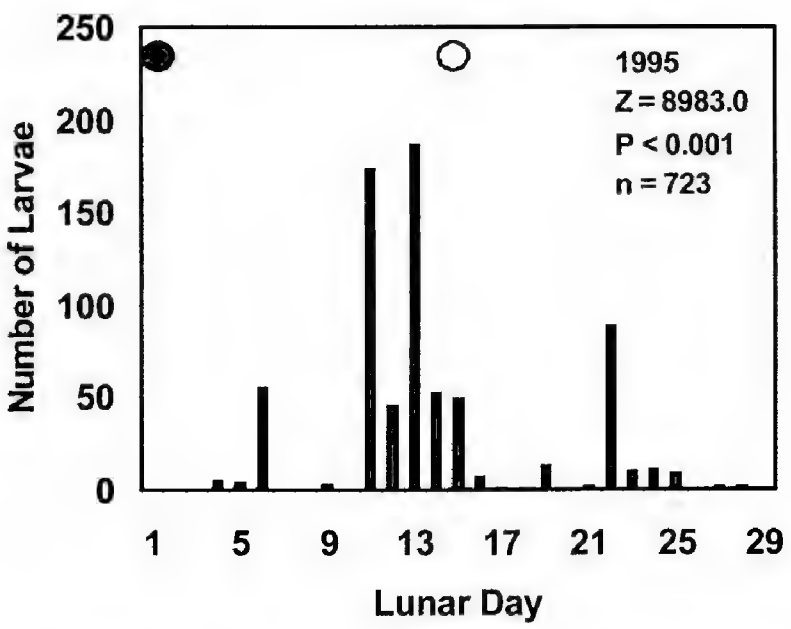


Figure 9. Lunar cycle of larval *M. atlanticus* catches made in Sebastian Inlet, Florida, during summer 1995. Rayleigh's test of circular distributions (Z = 8983.0, P<0.001) indicates a non-uniform hatching distribution throughout the lunar months. Closed circle = new moon; open circle = full moon.

Figure 10. Scanning Electron Micrograph of a sagittal otolith of *M. atlanticus* with an estimated age of 20 days.

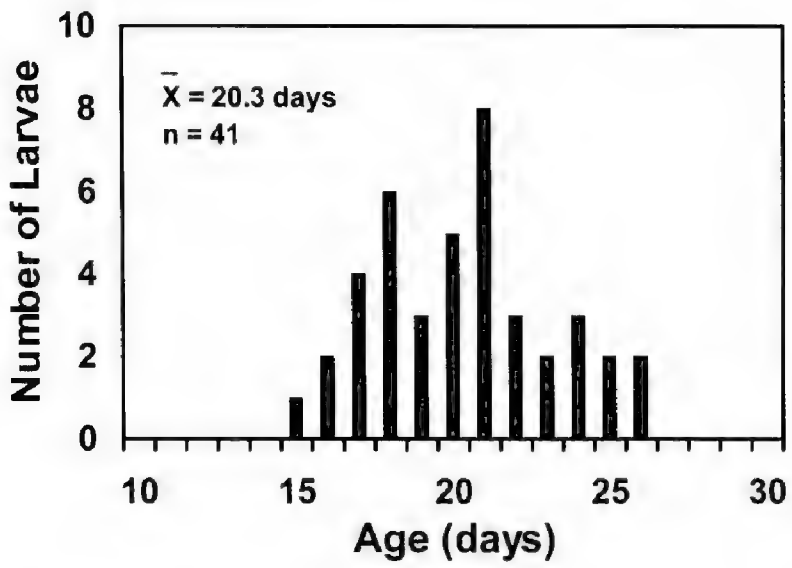


Figure 11. Age distribution of *M. atlanticus* captured while immigrating through Sebastian Inlet, Florida.

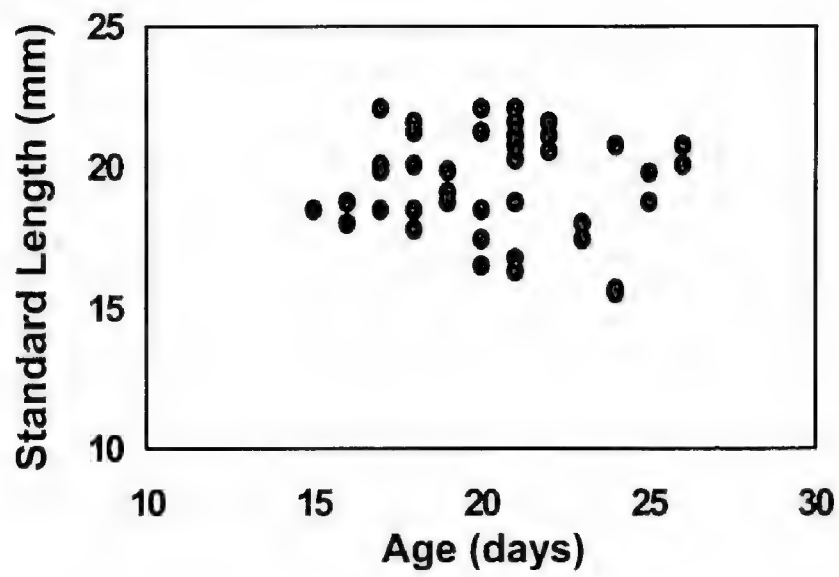


Figure 12. Age/length relationship of *Megalops atlanticus* captured while immigrating through Sebastian Inlet, Florida.

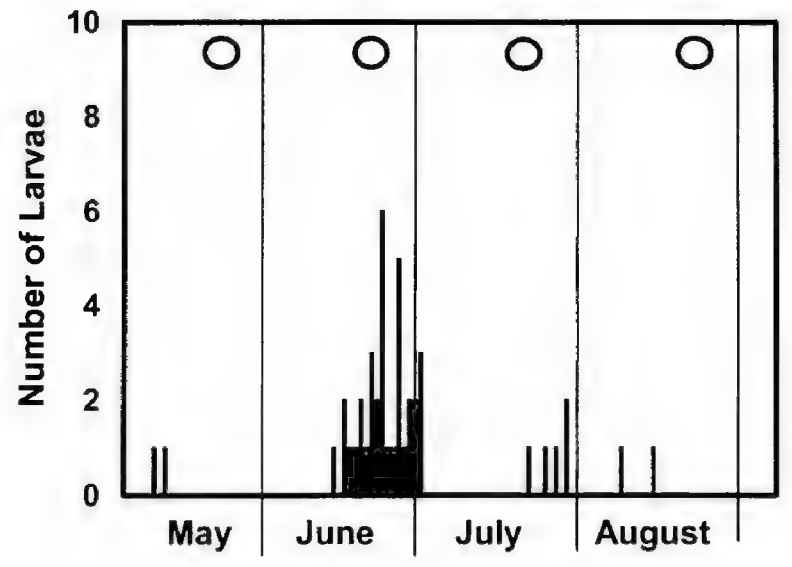


Figure 13. Estimated hatching dates of *Megalops atlanticus* captured in Sebastian Inlet, Florida, summer 1994. Open circles = full moons.

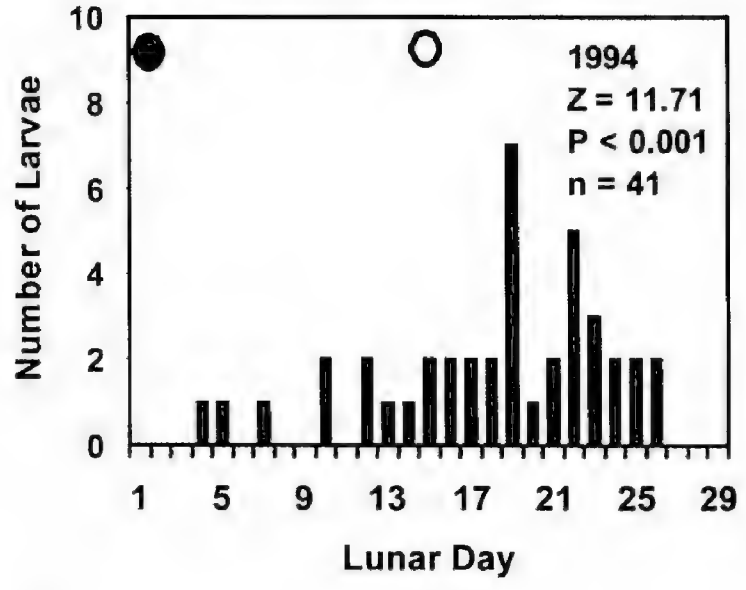


Figure 14. Lunar periodicity in hatching dates for 41 *Megalops atlanticus* larvae captured in Sebastian Inlet, Florida, summer 1994. Rayleigh's test of circular distributions ($Z = 11.71$, $P<0.001$) indictes a non-uniform hatching distribution throughout the lunar months. Closed circle = new moon; open circle = full moon.

season can extend at least into late September. Ferrell (1999) examined the transport of a broad spectrum of fish larvae through Sebastian Inlet in the fall season by deploying a 1 m diameter plankton net from a catwalk below the bridge spanning the inlet. This net was fished for the first two hours of nocturnal flood tide for 21 nights in September and October, 1998. Specimens were preserved in formalin, precluding subsequent otolith analysis. When samples were processed later that fall and winter, a total of 100 *M. atlanticus* larvae were found, with recruitment occurring as late as 22 October. These larvae ranged from 11-24 mm SL, with a mean size of 17.8 mm SL.

## DISCUSSION

Recruitment of *Megalops atlanticus* into the estuarine environment of the IRL was highly episodic throughout the two years of study. Analysis of the patterns of recruitment may assist in the evaluaton of mechanisms that affect inter-annual variability of populations, and help develop management strategies for the critical estuarine nursery habitats utilized by this and other species.

The three-fold difference in the magnitude of recruitment between years, and patterns observed within each summer, indicates that recruitment of *M. atlanticus* is strongly influenced by both biotic and abiotic factors. The initial pattern that appears in the data is that recruitment peaks are cyclical, with the major peaks in larval entry into the IRL occurring during the week prior to the full moon. This pattern presumably reflects the reported lunar cycles in the spawning behavior of adult *M. atlanticus*. Based on analysis of otoliths taken from larvae caught off the west coast of Florida, Crabtree (1995) detected a bimodal lunar cycle in hatching date, with peak hatching activity occurring on 6-7 days after the full moon, and a lower level of spawning activity 3-8 days after the new moon. Assuming a 2-3 day egg incubation time, peak spawning activity in that region thus occurred shortly after the full and new moons of May, June and July. Otolith analysis of a subsample of the larvae taken in this survey indicates a larval age of 15-26 days at recruitment (mean - 20.2 days). Most of these recruiting larvae were thus the product of spawning that occurred on or shortly after the preceeding full moon. Secondary peaks in the lunar distributions of larvae recruiting into Sebastian Inlet in both 1994 and 1995 provide some evidence of bimodal spawning activity among the adult *M. atlanticus* that produced the larvae collected in this study.

Recruitment in 1995 was dramatically higher (n=723) than in 1994 (n=243), possibly reflecting the influence of abiotic processes that may have affected larval survival and transport to the inlet. The absence of strong weather events in 1994 suggest that larvae relied on prevailing current patterns, with perhaps some oriented swimming (Stobutzki and Bellwood 1998), to assist their return to the coastal waters and entrainment into tidal

currents flooding into the IRL. The initial recruitment peak in early 1995 was also not associated with any meterological driving forces. However, by far the greatest episode of recruitment observed during the entire study occurred in early August, and was associated with the passage of Hurricane Erin.

Hurricane Erin was a Category 1 storm that approached the coast from the ESE. Our last samples were collected at 0900-1100 on 31 July, about 6 hours before winds associated with the storm began to reach the coast. Because landfall was initially expected to be considerably to the south of the study site, we did not remove the nets from the moorings, and they remained in place throughout the period. With peak winds reaching 38 m/sec (85 mph), the eye of the hurricane passed directly over Sebastian Inlet. A sharp 30 mb drop in atmospheric pressure was observed at the park's weather station as the eye made landfall. Because of the intense squall activity following the hurricane, we were not able to get back on the IRL until 2 days after passage of the storm. The first day was devoted to recovering and cleaning the nets, which were almost completely filled with debris. The next 5 days generated catches of up to 175 larvae/day, far exceeding any previous episodes of recruitment than had previously been detected.

Despite the apparent relationship between the hurricane and larval transport into the IRL, the recruitment pulse actually began prior to the storm. A small number of larvae were captured 2-3 days before the hurricane, and 50 larvae were taken during our last sampling before the storm. Several hypotheses can be proposed to explain this pattern: 1) a very large larval cohort was being advected into the vicinity of the inlet during a week of light onshore winds, and the nearly simultaneous occurrence of the hurricane was simply a coincidence; 2) the hurricane winds and atmospheric pressure fields compressed the pre-existing patch of larvae against the coastline where they could be entrained into the inlet over the week after storm passage; 3) the advancing hurricane pushed water ahead of it towards the coast, driving larvae from offshore waters into the coastal zone prior to the storm. Wind and wave-associated Stokes Drift does indeed propagate in front of a moving storm (Knauss 1997). Calculations of the magnitude of the Stokes Drift in front of a storm with the wind speed and rate of forward motion of Hurricane Erin indicate that, in a boundary-less ocean, it can displace the surface water by up to 30 km at least 24 hours in advance of the storm (pers comm., G. Maul, Florida Institute of Technology, Division of Marine and Environmental Systems, Melbourne, FL). The presence of a shoaling coastline would reduce the Stokes Drift, but it still may be able to enhance the shoreward drift of a patch of larvae in front of the storm.

The source of larvae recruiting to Sebastian Inlet and their transport pathways to the coast, were not examined in this research, but these questions are vital components of the population dynamics of the species. Adult *M. atlanticus* are common in the IRL and

along the adjacent ocean beaches, but their spawning sites and potential contribution to the larval pool recruiting to the IRL remain undetermined. Previous research has found recently hatched larvae off the west coast of Florida and at sites near southern Mexico (Smith 1980; Crabtree 1995). Small larvae have occasionally been found in ichthyoplankton surveys off North Carolina (Berriens et al. 1978).

Sebastian Inlet is located at the southern end of the South Atlantic Bight, which extends from Cape Hatteras to West Palm Beach (Pickard and Emery 1990). The northward-flowing Gulf Stream, which diverges from the Florida coast at West Palm Beach, is found approximately 40 km east of Sebastian Inlet. The complex interactions among oceanographic features of the central Florida coast suggest several hypotheses about larval origin and transport.

Several hypotheses regarding the spawning locations of *M. atlanticus* that recruit into the IRL can be proposed. Larvae potentially can originate as far away as southwest Florida, where Crabtree et al. (1992) found newly-hatched fish. If larvae spawned at that location are entrained into the Loop Current and Gulf Stream, they can potentially be transported around peninsular Florida and as far as Sebastian Inlet during their 15-25 day larval lives. Meanders occurring along the westward edge of the Gulf Stream may help larvae reach the shore. Alternatively the spawning area may be located closer to Sebastian Inlet, with the southward or oscillating flow inshore of the coastal frontal zone providing a local retention mechanism that enables larvae to enter coastal estuaries. A final possibility may be that spawning occurred elsewhere in the Caribbean and larvae were carried by the Antilles Current to the Gulf Stream.

Once larvae reach the estuarine ecosystems, they travel to nursery habitats deep within marshes lining the estuaries. These marshes are often characterized by very poor water quality and low dissolved oxygen levels, which does not inhibit their utilization by juvenile *M. atlanticus* that inhale air into their highly vascularized swim bladder (Geiger et al. 2000). Juveniles can be very abundant in IRL marshes adjacent to inlets, with catches of up to 250 fish being made in a single seine haul taken in deep potholes, depressions and dredged canals in unmanaged marshes that remain open to the IRL throughout the year (Shenker, unpubl. data). During the fall of 1995, in the aftermath of Hurricane Erin, large numbers of juveniles were observed in marshes in the northern IRL that are located more than 50 km from the nearest inlet (D.S. Taylor, Brevard County Mosquito Control District, pers. comm.). The IRL is primarily a non-tidal system at locations more than 10 km from an inlet, and water flow generally is wind-driven. It seems likely that hurricane-driven circulation may have helped disperse larvae throughout the inlet. Interestingly, the present study is not the first to link *M. atlanticus* recruitment into remote marshes by hurricanes. Breder (1944) reports on numerous

instances in which juvenile *M. atlanticus* have been found in remote headwaters and marshes, and wrote: "It has long been suspected that small tarpon may get into the odd places in which they are sometimes found by being driven in on the wings of a hurricane or late summer storm."

## ACKNOWLEDGEMENTS

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# ISLA CONTOY- A MEXICAN CARIBBEAN ECOSYSTEM USED BY TARPON, *MEGALOPS ATLANTICUS* AS A FEEDING AREA

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## ABSTRACT

Contoy Island, also known as Bird Island, is a National Marine Park located north of the Yucatan Peninsula in the Mexican Caribbean. Several studies have been conducted to characterize biodiversity within the park, however, neither fish populations nor the ecological function of its coastal lagoons have been studied. With these objectives in mind, bimonthly fish sampling and the collection of physical parameters from the various lagoons Old Port, North, Central Pajarera, Garzas, and the coastal area of the park (Fisherman camp, Cocopatos and South End) were undertaken from April 1999 to January 2000. A total of 92 fish species belonging to 41 families and 62 genera were collected with tarpon, *Megalops atlanticus* being the 10th most dominant species on a biomass basis. *Megalops atlanticus* uses these lagoons as feeding areas during dry and rainy seasons when nutrients are high and oxygen levels are low. Stomach content analysis showed a high preference by juvenile tarpons for benthic organisms within the lagoons, mainly invertebrates. Study results provide an important contribution to the knowledge of tarpon biology in the Mexican Caribbean.

## INTRODUCTION

Tarpon, (*Megalops atlanticus)* a large, long-lived (48 years), migratory elopomorph fish, occurs in coastal and inshore waters of the tropical and subtropical Atlantic (Crabtree et al, 1997). The western Atlantic assemblage is distributed from Virginia's eastern shore to central Brazil throughout the Caribbean Sea and Gulf of Mexico (Hildebrand, 1963; Zale and Merrifield, 1989). Extremely euryhaline, tarpon have been captured 200 km upstream in limnetic environments and reportedly spawning in neritic waters (Castro-Aguirre et al, 1999). The economic importance of tarpon as a prime inshore game fish with great potential for aquaculture has been widely known (Hoese and Moore, 1998).

Although tarpon has little food value, its extraordinary strength and spectacular jumping ability has placed them into a position of prominence in the sport fishing world

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(Zappler, 1993). However, the collapse of this important sport fishery in 1960 has been a source of concern not only to fisherman, but also to fisheries scientist and conservation groups. Diverse nations have considered as a national priority to increase the understanding of the biology, ecology, and population dynamics of this sport-fishing species to develop conservation actions which may improve existing populations.

Most of the research about tarpon ecology and biology has been conducted in Florida and South America. Population studies in the Caribbean have listed it as a common species in the Hondo River of Quintana Roo, Mexico (Schmitter, 1998) and rare in reef waters (Macías, 1991; Tunnell et al, 1993; Gutierrez-Carbonell et al., 1993). Recent studies suggest a seasonal abundance pattern in Caribbean reefs (Ordóñez, 2000). However, additional biological studies are required to assess spawning areas and the abundance and distribution of juvenile tarpon. This research is basic to estimate tarpon population size and the location of recruitment, feeding and nursery areas. This information is needed to coordinate conservation and management actions shared by different countries.

With this in mind, in this study we investigated the spatial and temporal abundance of the tarpon *M. atlanticus* within a fish community occurring in a protected marine reserve in the Yucatan Peninsula, Contoy Island and adjacent waters, where no fishery action is allowed. The results are correlated with environmental parameters and feeding preferences to identify habitat and hydrographic preferences.

## Study Area

Contoy Island, also called Bird Island, is one of the protected marine areas of the Mexican Caribbean located north of the Yucatan Peninsula, between the Caribbean and the Gulf of Mexico (21°27'-21°32' N and 86°46'-86°47' W). It was decreed a National Marine Park in 1998 as a refuge with good feeding grounds and nursery areas for marine birds (96 species and three subspecies), reptiles (turtles), invertebrates such as the spiny lobster, 106 benthic reef species and diverse marine, estuarine and freshwater fishes (Programa de Manejo, 1997).

This irregularly shaped park is 8.8 km long, varying in width from 20 m in the extreme north to 700m in the center, with a surface area of 238 ha of which 3.4% are coastal lagoons (Figure 1). The rocky eastern littoral is strongly eroded without beaches, while the western side has sandy and rocky zones whose beaches are cut by narrow inlets such as North Lagoon, Dead Lagoon (in process of drying), Old Port Lagoon, Pajarera Central, Laguna Garzas and Pajarera South. All these lagoons are bordered by mangroves and filled with turbid water, with some of them fed by underground seeps giving the system an estuarine character that promotes habitat heterogeneity and rich biodiversity.

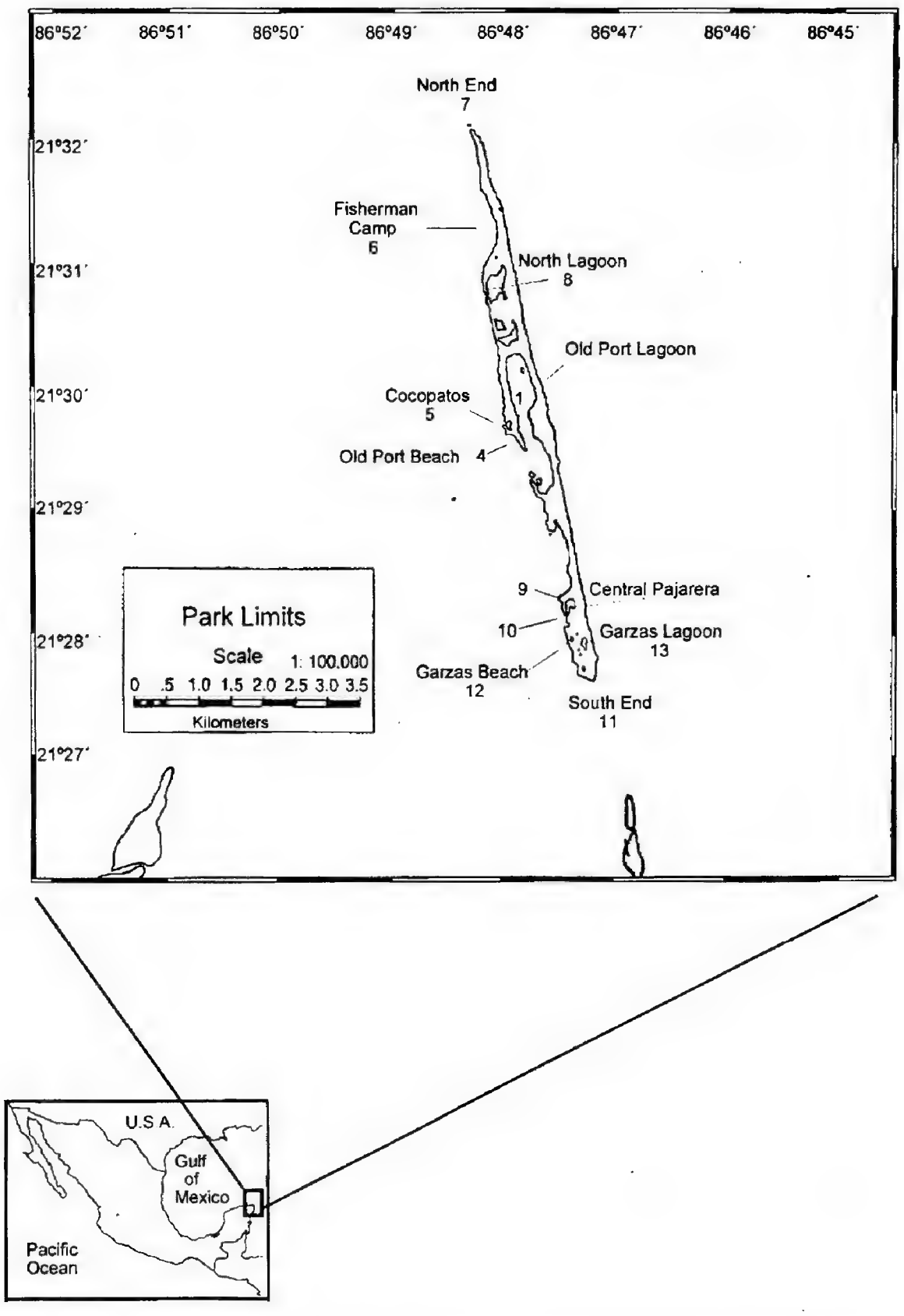


Figure 1. Study area located north of the Yucatan Peninsula showing the sampling stations

## MATERIALS AND METHODS

Bimonthly fish sampling was carried out from April 1999 to January 2000 at ten sampling stations, including coastal systems and beach areas, using a 30 m long x 2 m wide beach seine with 2.54 cm mesh size, sweeping an estimated total area of 582 $m^2$. At each station, at least two replicates were made following Lager (1978). Water physical parameters (temperature, salinity, dissolved oxygen) were measured with an 85 YSI meter and water samples collected for nutrients analysis at the Chemistry Laboratory of CINVESTAV-Unidad Mérida. All fishes were immersed in, and their abdominal cavities injected with, a 15% formalin solution in seawater. The specimens were transported to

the laboratory where they were washed, sorted and identified. Individual wet weights (g) and length measurements (SL) in cm were recorded for each specimen.

Spatial and temporal distributions were determined according to their numerical and weight abundance, numbers and wet weight were registered for each sampling station. Relationships between biotic and abiotic factors were estimated by Pearson correlation coefficient with an $\alpha = 0.05$.

Stomach contents were examined under a dissecting microscope and identified to the lowest possible taxon. Food items were recorded quantitatively and diet composition analyzed by gravimetric method (Hyslop, 1980) with results expressed as percentage of total stomach content.

## RESULTS AND DISCUSION

Spatial physical and chemical parameters varied greatly; nitrites and nitrates consistently yielding low values at all locations, proved to be an exception (Table 1). These results agree with Lalli and Parsons (1993) who emphasize that nitrogen is the major limiting nutrient for plant growth in marine environments. High phosphorus and silicate were found in Pajarera Central Lagoon during the rainy season (September), probably due to bird guano and the proximity to freshwater springs, low dissolved oxygen levels may indicate high eutrophication.

Table 1. Average hydrological parameters ± (standard deviation) registered in the sampling stations during the study period (April-1999 to January 2000). Temp.: temperature, sal: salinity, De: Depth, $O_2$: dissolved oxygen, $NH_4$: ammonium, $NO_2$: nitrites, $NO_3$: nitrates, $PO_4$: phosphates, $SiO_4$: silicates.

| Station | Temp(°C) | Sal.(‰) | De(m) | $O_2$(mg/l) | $NH_4$(µM) | $NO_2$(µM) | $NO_3$(µM) | $PO_4$(µM) | $SiO_4$(µM) |
|---|---|---|---|---|---|---|---|---|---|
| Old Port | 28.8 (4.0) | 39.2 (7.4) | 1.4 (0.6) | 7.9 (4.0) | 2.8 (1.0) | 0.1 (0.1) | 0.3 (0.2) | 0.4 (0.3) | 5.5 (2.2) |
| Old Port Beach | 29.4 (3.5) | 37.0 (0.5) | 0.7 (0.2) | 8.2 (3.5) | 2.2 (0.9) | 0.1 (0.1) | 0.3 (0.2) | 0.2 (0.2) | 4.5 (1.7) |
| Cocopatos | 28.7 (3.0) | 36.7 (0.3) | 0.5 (0.2) | 6.4 (3.1) | 4.2 (2.7) | 0.1 (0.1) | 0.4 (0.2) | 0.5 (0.3) | 3.9 (1.2) |
| North Pajarera | 28.4 (2.7) | 37.3 (0.5) | 0.6 (0.3) | 7.4 (1.8) | 5.9 (2.0) | 0.2 (0.1) | 0.3 (0.2) | 0.7 (0.3) | 3.4 (0.8) |
| Central Pajarera | 26.8 (3.2) | 38.7 (0.5) | 0.7 (0.1) | 3.8 (1.8) | 4.0 (0.6) | 0.5 (0.5) | 0.5 (0.5) | 6.3 (2.0) | 6.5 (2.4) |
| P. Central Inlet | 27.1 (2.5) | 37.3 (0.4) | 0.8 (0.1) | 5.7 (3.2) | 5.3 (2.2) | 0.2 (0.1) | 0.5 (0.3) | 1.0 (0.8) | 3.7 (3.0) |
| South End | 25.3 (2.7) | 36.9 (0.3) | 1.6 (0.6) | 5.8 (1.2) | 2.5 (0.7) | 0.04 (0.01) | 0.2 (0.04) | 0.1 (0.1) | 3.7 (3.0) |
| Garzas Beach | 27.2 (2.5) | 36.9 (0.2) | 0.6 (0.2) | 5.7 (1.6) | 2.8 (1.3) | 0.1 (0.04) | 0.2 (0.03) | 0.2 (0.1) | 4.1 (2.1) |

In general, Old Port and Pajarera Central and other coastal semi-enclosed lagoons exhibited warm water, high salinity and silicate levels and low dissolved oxygen. Colder waters with low salinity and nutrient levels and high oxygen levels characterized stations (Garzas Beach, Cocopatos, Pajarera Central Inlet and South End) exposed to the open sea and those located on the southern side of the Island.

A total of 20,470 fishes, belonging to 92 species and 42 families were caught. The families Scaridae, Gerreidae and Syngnathidae were the most common and represented 23% of the total species captured. Numerical abundance was highly dominated by *Floridichthys polyommus* (28.1%) followed by *Eucinostomus argenteus* (12.4%). In terms of biomass, 10 species were the most representative (72%) with *Lactrophrys quadricornis,* followed by *F.* pol*yommus*, as dominants (Table 2). Tarpon, *Megalops atlanticus* made up 2.8% of the total fish weight (Figure 2), however, it is important to mention that although several tarpon were observed in the lagoons, only 6 juveniles, 33 and 42 cm SL, were captured in Pajarera Central.

Coastal lagoons are highly eutrophicated because of fertilization by bird guano and are utilized by tarpon and other fish species (*Lutjanus spp.)* as a feeding area. This environmental characteristic prevents juvenile tarpon from being preyed upon by predators. This is reflected in Table 3, where tarpon occurrence showed strong positive correlations with phosphates, nitrites and silicates, reaching significant values of 0.99, 0.91 and 0.80, respectively and a negative correlation with oxygen (-0.70). Tarpon can utilize these areas because the open connection of its swim bladder with the gullet provides an adaptive advantage for air breathing in anoxic environments. Other species showing similar significant correlations with nutrients and oxygen levels are the gerrids *Eucinostomus argents* and *Diapterus rhombeus*.

Temporal analysis showed that captures during June (dry season) when dissolved oxygen level was low (2.5 mg/l), and in September (rainy season), when phosphates and silicates were high (9.1 and 9.3 μM, respectively) the highest biomass was registered (Figure 3). Crabtree et al., (1997) reported that tarpon spawn seasonally (April-August) in Florida and throughout the year in Costa Rica. Because of this disparity in spawning periodicity and the variation between overall size and size at sexual maturity in both areas, these authors suggest a limited displacement mixing of fish between the two areas. Due to these differences, Crabtree suggested a possible mechanism for tarpon larvae produced in the Caribbean to be recruited into Florida waters (Crabtree et al., 1992).

Although only the stomach contents of six juveniles (33 and 42 cm SL) were analyzed, the results are an important contribution to the life history of tarpon because of the paucity of available data. All the specimens collected were juveniles feeding primarily on benthic microcrustaceans. Amphipods, of the genus *Corophium*, harpacticoidea copepods and fishes (Gerreidae) were the main trophic groups identified from stomach contents.

Table 2. Total density (No.100m$^{-2}$) and biomass (g.100m$^{-2}$) registered for dominant fish species collected in Contoy Island.

| SPECIE/STATION | Old Port | Old Port Beach | Cocopatos | North Lagoon | Fisherman Camp | Central Pajarera | Pajarera inlet | South End | Garzas Beach |
|---|---|---|---|---|---|---|---|---|---|
| *Floridichthys polyommus* | 10.1 (26.3) | 450.7 (775.0) | 585.7 (1,235.5) | 820.0 (1,340.0) | 6.8 (42.1) | 512.8 (361.1) | 0.0 (0.0) | 0.0 (0.0) | 41.6 (347.3) |
| *Lactrophrys quadricornis* | 0.3 (156.3) | 1.4 (364.6) | 2.0 (409.9) | 0.0 (0.0) | 1.7 (463.4) | 0.0 (0.0) | 13.4 (5,333.2) | 0.0 (0.0) | 0.7 (1,123.9) |
| *Atherinomorus stipes* | 416.0 (154.3) | 116.6 (87.3) | 287.4 (139.3) | 0.0 (0.0) | 0.0 (0.0) | 21.5 (3.8) | 244.8 (195.0) | 0.0 (0.0) | 242.1 (199.5) |
| *Harengula jaguana* | 3.4 (25.3) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 236.6 (287.9) | 1.7 (3.1) | 71.2 (450.6) | 0.0 (0.0) | 323.6 (543.9) |
| *Ecinostomus argenteus* | 0.9 (1.0) | 2.7 (4.2) | 153.4 (342.9) | 198.7 (233.3) | 2.1 (14.9) | 224.0 (225.4) | 61.7 (50.8) | 0.0 (0.0) | 95.8 (100.0) |
| *Cathorops melanopus* | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 4.1 (2,611.9) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) |
| *Ariopsis felis* | 0.0 (0.0) | 0.0 (0.0) | 0.3 (29.6) | 2.1 (84.7) | 6.1 (533.3) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) |
| *Lutjanus griseus* | 1.9 (63.9) | 2.0 (56.3) | 0.0 (0.0) | 0.3 (0.3) | 0.0 (0.0) | 9.9 (504.3) | 17.8 (2,762.8) | 0.1 (0.1) | 0.3 (4.7) |
| *Haemulon sciurus* | 0.3 (7.8) | 1.7 (1.1) | 0.0 (0.0) | 0.0 (0.0) | 100.9 (44.1) | 0.0 (0.0) | 62.1 (2,400.0) | 0.1 (0.2) | 0.0 (0.0) |
| *Anchoa hepsetus* | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 14.3 ( 14.1) | 0.0 (0.0) | 120.7 (193.4) | 0.0 (0.0) | 1.4 (1.3) |
| *Megalops atlanticus* | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 1.7 (1,178.8) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) |

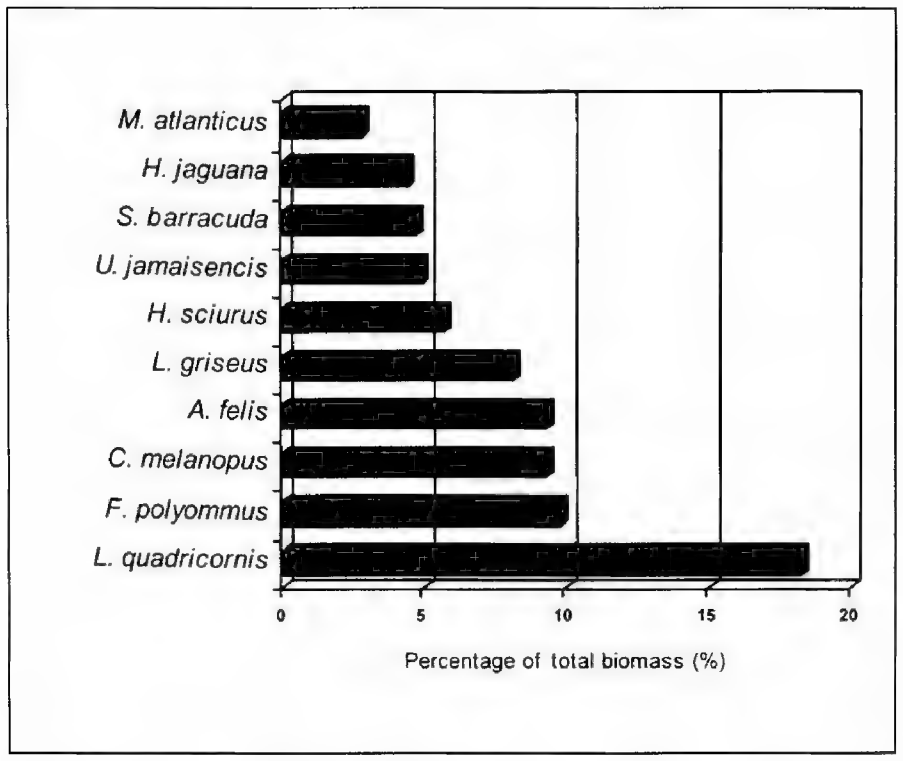


Figure 2. Dominant fish species by biomass captured at Contoy Island Marine Park, Quintana Roo, Mexico.

Table 3. Correlations coefficients between the average densities registered for some of the species collected in Isla Contoy and the environmental parameters. Correlations with $p<0.05$ are indicated*. $NH_4$: ammonium, $NO_2$: nitrites, $NO_3$: nitrates, $PO_4$: phosphates, $SiO_4$: silicates.

| Species | Salinity | Oxygen | Depth | $NH_4$ | $NO_2$ | $NO_3$ | $PO_4$ | $SiO_4$ |
|---|---|---|---|---|---|---|---|---|
| *Floridichthys polyommus* | -0.03 | -0.05 | -0.76* | 0.27 | 0.45 | 0.20 | 0.36 | 0.22 |
| *Lactrophrys quadricornis* | -0.25 | -0.09 | -0.14 | 0.31 | -0.10 | 0.29 | -0.17 | -0.33 |
| *Atherinomorus stipes* | 0.22 | -0.03 | -0.31 | -0.19 | -0.15 | -0.10 | -0.12 | 0.29 |
| *Harengula jaguana* | -0.48 | 0.02 | -0.16 | 0.04 | -0.26 | 0.24 | -0.25 | -0.40 |
| *Ecinostomus argenteus* | -0.01 | -0.58 | -0.81* | 0.69* | 0.61 | 0.41 | 0.49 | 0.10 |
| *Cathorops melanopus* | -0.28 | 0.42 | 0.30 | -0.03 | -0.12 | 0.43 | -0.13 | -0.30 |
| *Ariopsis felis* | -0.31 | 0.46 | 0.23 | 0.09 | -0.10 | 0.43 | -0.15 | -0.37 |
| *Diapterus rhombeus* | 0.49 | -0.71* | -0.26 | 0.12 | 0.91* | 0.56 | 0.98* | 0.78* |
| *Lutjanus griseus* | 0.38 | -0.53 | -0.17 | 0.37 | 0.59 | 0.54 | 0.56 | 0.39 |
| *Haemulon sciurus* | -0.05 | -0.18 | -0.07 | -0.41 | 0.05 | 0.27 | -0.05 | -0.20 |
| *Syngnathus floridae* | -0.15 | 0.47* | -0.34 | -0.05 | -0.16 | -0.24 | -0.23 | -0.12 |
| *Anchoa hepsetus* | -0.27 | 0.16 | 0.17 | 0.29 | -0.05 | 0.55 | -0.13 | -0.40 |
| *Megalops atlanticus* | 0.53 | -0.70* | -0.21 | 0.10 | 0.91* | 0.54 | 0.99* | 0.79* |

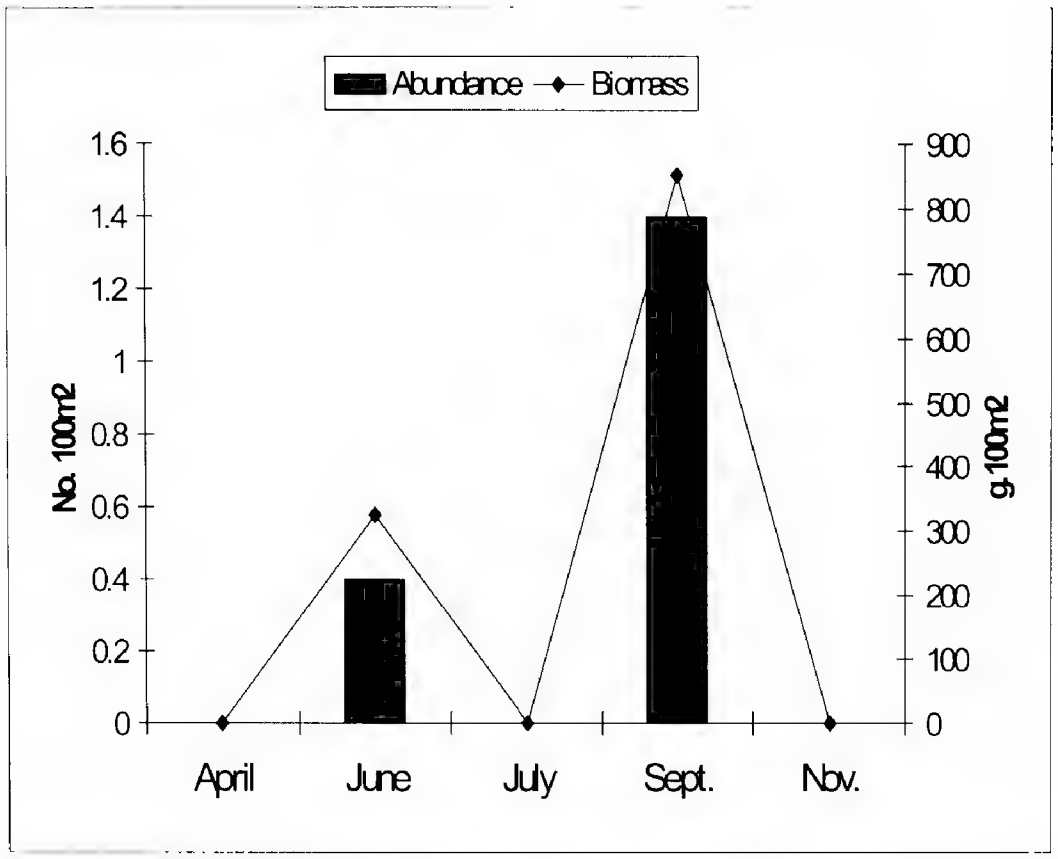


Figure 3. Monthly average abundance and biomass measured for tarpon *Megalops atlanticus* in the coastal system from Contoy Island

*Corophium* amphipods provided the major food source, representing 65% of the total stomach content (Figure 4). This is not surprising, as amphipods are extremely abundant because of the high content of organic matter in coastal systems. Gerrids, which have been considered to be microcrustacean feeders in a previous study conducted in the Yucatan Peninsula (Vega et al., 1994), were also abundant where extremely low oxygen prevails.

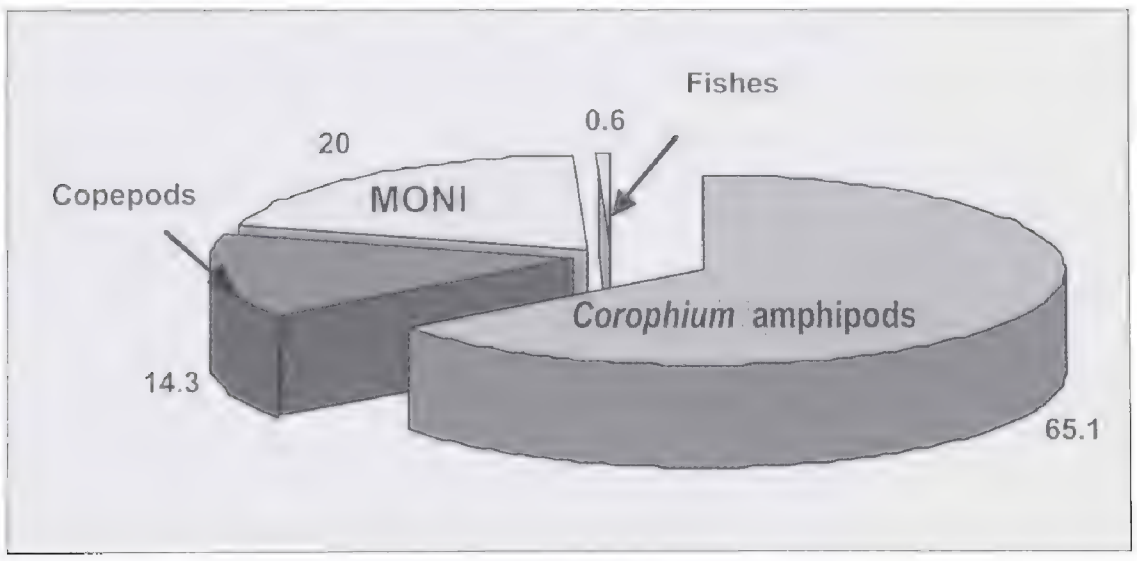


Figure 4. Percentage contribution to weight of the principal food resources for *Megalops Atlanticus* collected in Isla Contoy, Quintana Roo. MONI: Organic Matter not identified

Previous studies state that tarpon is an opportunistic predator, preying upon crabs, shrimps and other fish (Zappler, 1993). Cataño and Garzín Ferrera (1994) studying the feeding habits of this species, found that insects are not an important prey, while fishes of the Families Mugilidae and Poecilidae represented more than 80% (by weight) of the

total stomach contents. On the other hand, Chacon-Chaverri (1994) found that juveniles (1.5-9.0 cm SL.) feed mainly on copepods and insects, while conspecifics >27.0 cm SL tend to primarily consume fishes. Our study found that fishes were not an important food in juveniles larger than 27 cm. This disparity may result from the small sample size.

Qualitative and quantitative variations in tarpon feeding habitats are due to resource availability, seasonality, locality, hydrology and size and age of the fish (Hyslop, 1980; Prejs and Colomine, 1981). Cyclic fluctuations in food accessibility and composition may force juvenile to be more opportunistic in their diet. In this sense, growth and survival is a reflection of the abundance and availability of food resources.

## CONCLUSIONS

- Island Contoy richness in fish biodiversity is likely due to its location in the transition zone between the Gulf of Mexico and Caribbean waters.
- Tarpon were distributed spatially and temporally within the coastal systems where anoxic conditions and high nutrient levels prevail.
- Lowest oxygen levels and highest nutrient (phosphates and silicates) levels were found during dry and rainy season, respectively. These extremes are coincident with the occurrence and highest tarpon abundance.
- Fertilization of the water by bird guano promotes high primary production resulting in abundance of organic matter.
- Tarpon inhabit these systems as feeding area with benthic microcrustaceans as the principal food source.

## ACKNOWLEDGEMENTS

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# LIFE HISTORY STRATEGIES, POPULATION DYNAMICS, AND CONSEQUENCES FOR SUPPLEMENTAL STOCKING OF TARPON

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## ABSTRACT

Release of hatchery-reared fish is viewed as a potential means to supplement coastal fish stocks, yet the viability of such programs has not been explored either theoretically or empirically. Here we examine implications from life history theory and results from population simulation models to examine the relative impact of alternative ecological and management scenarios on tarpon abundance. Life history theory predicts that "periodic species" (long-lived organisms with high fecundity) should experience large inter-annual variation in recruitment in response to density-independent environmental factors that operate on large scales. Because tarpon possess periodic life-history attributes, population dynamics should reflect strong recruitment episodes that ultimately are driven by climatic/environmental variation. Density-dependent mechanisms probably influence growth and survival of early life stages only during intermittent periods of high recruitment success. To examine these ideas, we configured an age-based matrix model to reflect tarpon life history. We simulated 50-year time series with or without density dependence and with or without supplemental stocking of early or late juvenile fish. Stocking large numbers of age-30 d fish had a negligible effect (1% change) on the abundance of age 20-22 fish, a typical adult cohort, but the addition of density dependence caused a 35% average decline in cohort abundance. Stocking large numbers of age-65 d fish increased the abundance of the age 20-22 cohort by 8%, but this benefit disappeared under an assumption of density dependence. Stochastic inter-annual variation in larval survival had a large negative effect on population abundance. Because life history theory predicts that tarpon should be strongly influenced by large-scale environmental variation, supplemental stocking would be more effective when fish are released at advanced size/age and when environmental conditions dictate low natural recruitment. Even stocking at advanced age could have uncertain and marginal benefits. Changes in survival rates of early life stages had a much greater effect on population abundance than either supplemental stocking or density dependence. A 1% increase in survival rate of any given early life stage caused a tenfold increase in adult cohort

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abundance. To increase tarpon stocks, protection of adult breeding stocks and restoration/enhancement of coastal habitats essential for juvenile tarpon provide a more viable strategy than supplemental stocking.

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## INTRODUCTION

Prior to the 1960s, tarpon (*Megalops atlanticus*) were abundant in Texas and supported a thriving sportfishery at Port Aransas and several other coastal locations. The decline and virtual disappearance of tarpon from Texas coastal waters during the 1960-70s was poorly documented and has not been explained, although many theories have been proposed. In recent years, tarpon began to appear in Texas waters during the summer, but catch rates remain far below values reported during the period 1930-1960, and most tarpon are encountered offshore. Much interest now exists for the reestablishment of a tarpon sportfishery in Texas coastal waters. A management option discussed with increasing frequency is population enhancement via supplemental stocking with hatchery-reared fish. Because the fates of hatchery-reared fish and their contributions (relative to natural production) to adult stocks remain undocumented, stocking programs for enhancement of marine fish populations are controversial (Grimes 1998).

Here we examine the potential for supplemental stocking to enhance tarpon populations. We base our analysis on life history theory: the manner in which populations with different reproductive and demographic characteristics respond to environmental variation. We first review fundamental relationships between life history strategies and population dynamics in response to environmental variation. We rely heavily on the triangular model of life history evolution developed by Winemiller and Rose (1992). We then summarize the life history attributes of the tarpon and place it within the framework of the triangular model. Finally, we report results from a series of matrix model simulations that examine the relative effects of supplemental stocking, density dependence, and recruitment variation on population abundance.

### Life History Theory and Population Dynamics

Life-history strategies result from correlations among organismal characteristics that affect fitness (reproduction and survival). Comparative studies have produced a robust pattern of life-history strategies observed among fishes, with three primary life-history strategies defining the endpoints of a triangular continuum (Winemiller 1992, Winemiller and Rose 1992). One endpoint, the opportunistic strategy, is defined by early maturation at small sizes, production of small clutches of eggs or embryos at frequent intervals, and long reproductive periods. A second endpoint, the equilibrium strategy, is characterized by production of relatively small clutches of large eggs, extended periods of spawning or

gestation, and well-developed parental care. A third endpoint, the periodic strategy, is associated with fishes that delay maturation until achieving intermediate or large size, produce large clutches of small (often pelagic) eggs and larvae, and have high mortality and growth rates during early life stages. Tarpon clearly possess the features of a an extreme periodic strategists (outlined below).

According to the triangular model, the opportunistic-strategy is associated with high maximum intrinsic rate increase ($r_{max}$) and rapid population turnover. Populations with early maturation, high reproductive effort, and high $r_{max}$ should be efficient colonizers and thus common in frequently disturbed habitats (e.g., mosquitofish, *Gambusia* spp.). These populations also can compensate for high adult mortality. Thus, these populations are resilient and the opportunistic strategy should be favored in dynamic (especially stochastic) habitats (e.g., coastal marshes) and in the face of high predation risk.

Equilibrium fishes are larger and more advanced at the onset of independent life. Marine ariid catfishes (oral brooding of a few large eggs) and live bearing fishes with long gestation periods and large neonates (e.g., many sharks) exemplify the equilibrium strategy. The equilibrium strategy should be favored in resource-limited, density-dependent settings (e.g., K-selection model of MacArthur and Wilson 1967). Compared with opportunistic and periodic strategists, equilibrium strategists should have lower recruitment variation and conform better to stock-recruit models. Low fecundity in equilibrium strategists is compensated by higher survivorship, especially among early life stages.

Tarpon and other periodic-strategists gain two benefits from delayed maturation and large adult body size: the capacity to spawn large numbers of eggs, and enhanced adult survival (larger fishes escape a wider range of gape-limited predators and can migrate further faster). Periodic fishes respond to large-scale spatial heterogeneity by spawning huge numbers of pelagic eggs, at least some of which thrive once favorable locations or periods are encountered. Even so, survival rates of early life stages are extremely low and variable (Bailey and Houde 1986, Rothschild 1986). The relatively few fortunate larvae that encounter areas of high resource density may achieve rapid growth. Coastal upwellings, gyres, convergence zones, and other oceanographic features create patterns of heterogeneity among physical parameters, primary production, and zooplankton densities. Estuaries used as nurseries by marine species are very heterogeneous. Large clutches of small pelagic eggs probably enhance dispersal capabilities, and increase the probability that at least some larvae will settle into suitable habitats. Over the long-term, mortality due to settlement in hostile habitats (advection) is balanced by survival benefits derived from recruitment of a certain fraction of larval cohorts into suitable regions or habitats (Winemiller and Rose 1993).

Life history tradeoffs associated with the triangular model can be derived from demographic relationships based on *r*, the intrinsic rate of natural increase (Southwood et al. 1974). We can approximate r as ln ($\Sigma l_x m_x$ )/T, where $l_x$ is age-specific survivorship, $m_x$ is age-specific fecundity, and T is mean generation time. Thus the growth rate of a population or lineage is directly influenced by tradeoffs among fecundity, survivorship, and the mean generation time. Other life history parameters have positive or negative correlations with these fundamental parameters (e.g., age of maturation is positively correlated with generation time). Averaged over many generations, $l_x$, $m_x$, and T must balance, or a population eventually will decline to extinction or grow exponentially.

Following this model, the periodic strategy corresponds to high fecundity, long generation time (delayed maturation), and low juvenile survivorship. Large body size not only enhances adult survivorship, but also allows storage of biomass/energy for future reproduction. Reproduction by periodic strategists often coincides with favorable conditions, when they occur, that facilitate growth and survival of early life stages. Correlations between parental stock densities and densities of recruits have been shown to be minimal in commercial marine stocks (Hilborn and Walters 1992, Rose et al. 2001), virtually all of which correspond to the periodic strategy. The periodic strategy typically is associated with high inter-annual recruitment variation in response to large-scale environmental variation, and generations are often recognized as discrete annual cohorts that may dominate populations of these long-live species for many years. Recruitment frequently depends on climatic conditions that influence water movement, egg/larval retention zones, productivity, and other environmental factors that determine early growth and survival (Rothschild 1986, Myers et al. 1990). For periodic fishes, the variance in larval survivorship that serves as input for models projecting population dynamics lies beyond the limits of precision and accuracy of field estimates. Even under the most favorable conditions, the great majority of eggs and larvae fail to survive for even a few days. Because recruitment is largely determined by unpredictable inter-annual and spatial environmental variation, the minimum stock density needed to ensure strong recruitment is impossible to determine with precision.

## Tarpon Life History

Despite the fact that tarpon (*Megalops atlanticus*) are one of the most popular sports-fish in the world, information on their life history and population dynamics have only been gathered recently (Cyr 1991, Crabtree et al. 1997). Tarpon possess all key characteristics of the periodic life-history strategy. Most Florida and Caribbean tarpon mature by about 10 years (0.8 – 1.2 m fork length, FL) and can survive for over 50 years (> 2.0 m FL), with females larger than males. Batch fecundity ranges from 1 million to over 20 million eggs, with larger females having higher fecundity according to the

relationship log(Fecundity) = 5.284 + 1.034 x log(Weight in kg) (Cyr 1991). Spawning is seasonal in Florida (April – July) and essentially year-round in Costa Rica (Crabtree et al. 1997). The number of spawning bouts per year by individuals is not known. Larvae may spend several months in the marine pelagic environment as nonfeeding leptocephali. Based on information for other periodic-type marine fishes, survivorship of larval tarpon is presumed to be extremely low. At about the time of metamorphosis to juvenile morphology, young tarpon drift or migrate into coastal passes (Shenker et al. 1995) and take up residence in coastal marshes where they remain for an unknown period (perhaps 1-3 years) before migrating between coastal inland and offshore waters. Survivorship of subadults and adults has not been estimated, but given the species' longevity is assumed to be high in the absence of fishing mortality.

## Simulation Models of Population Dynamics

Population dynamics can be modeled by a variety of conventions, each with its own strengths and limitations. Stock-recruit models are used to interpret recruitment dynamics based on adult stock abundance and assumptions about density dependence. The advantage of this approach is that little information is required about life history and ecology. The obvious disadvantage is that gross assumptions about density dependence are incorporated in a small number of parameters that define the predictive relationship. At the other end of the modeling spectrum are individual-based models, or IBMs. These population models often simulate life history and ecological relationships in great detail. The origins, survival, growth, and fates of individual organisms are modeled with varying degrees of detail. The great advantage of this approach is that numerous assumptions can be stated in detail at fine scales of resolution, which allows stronger interpretations about causal mechanisms (DeAngelis and Rose 1992). A major disadvantage of IBMs is the requirement for a great deal of ecological information in support of model development and testing.

An intermediate level of complexity for modeling population dynamics is obtained by age- or stage-based matrix models. Using Leslie Matrix projections, these models simulate population dynamics based on initial abundance, survivorship, and fecundity data for age classes or life stages. The basic Leslie Matrix model contains no elements of density dependence or environmental/demographic stochasticity. We modeled the population dynamics of a tarpon population using RAMAS-Age® (Akçakaya et al. 1999). This model employs several options to impose density dependence, migration, or stochastic influences on Leslie Matrix projections.

For our baseline condition, we first configured a tarpon population without influence from density dependence or significant demographic stochasticity (Table 1). The first age class combined the generalized hatchling and leptocephalus larval stages (1 - 30

days). The second age class combined postlarval and early juvenile early stages (30 - 65days). The third age class was late juveniles (65 days – 1 yr). The next two stages contained immature cohorts (2 - 4 and 5 - 7 yr). Each of the remaining 13 age classes contained units of 3 consecutive cohorts (8 - 10, 11 - 13, 44 - 46). Because mortality and survival rate information is lacking for tarpon, we estimated survival rates based on daily instantaneous mortality rate (M) estimates reported by McGurk (1986) for a variety of fish populations. Survival rate ($S_x$) = $N_t/N_0$, and $N_t = N_0e^{-Mt}$, where t is the time interval in days, $N_0$ is the intitial cohort, and $N_t$ is the number of survivors following interval t. For larval tarpon, we derived a survival rate of 0.000027 from M= 0.35 for *Scomber scombrus* on the Atlantic U.S. coast. For all other stages, we derived values of M from McGurk's dry weight – natural mortality rate regression (McGurk 1986, Figure 1). Following McGurk (1986), we assumed dry weight is 20% of wet weight.

We assumed an average wet weight of 5 g for early juveniles (yielding M = 0.0075) and 50 g for late juveniles (yielding M = 0.005). We estimated average wet weights of larger tarpon in various age classes from the relationship derived by Cyr (1991, Figure III-12). Average fecundity of each age class was derived from the empirical relationship reported by Cyr (1991): Fecundity = 372,540(Age in years).

To draw inferences about the potential influence of various ecological factors and stocking practices, we compared a series of simulated scenarios: 1) weak density dependence, 2) stochastic survival rate for the larval stage, 3) supplemental stocking of early juvenile or late juvenile fish, and 4) enhanced survival of larval, early juvenile, and late juvenile cohorts. The baseline condition together with various combinations of these four components yielded 18 simulated scenarios (Table 2).

Density dependence was simulated using the Beverton-Holt stock-recruit (or diminishing returns) function in RAMAS-Age ($Z= 1/(\rho + k/E)$, in which Z is number of recruits, $\rho$ is the reciprocal of the number of age-0 individuals produced, and k is a dimensionless parameter that determines the steepness of the function's ascent). Density dependence was simulated by setting $\rho = 1 \times 10^{-14}$ and k= 1.90.

A large stochastic influence on recruitment was simulated by setting the coefficient of variation (CV) for larval survival rate at 2.5 based on a normal distribution. Thus, in each time step of each simulation, larval survival changed to a new value randomly drawn from a normal distribution with a mean equal to the fixed value in the baseline scenario and CV = 2.5. This was the only stochastic feature of RAMAS manipulated for our simulations.

Table 1. Parameters used in the baseline matrix model simulation for tarpon population dynamics and variations used in 17 additional simulations. Survival rate estimates are based on data reported by McGurk (1986); fecundity data are based on data reported by Cyr (1991).

1. Baseline: no density dependence, no stochastic forcing, no stocking

| Age class | Initial abundance | Survival rate | Fecundity |
|---|---|---|---|
| 0 - 30 d | $5 \times 10^{12}$ | 0.000027 | 0 |
| 30 - 65 d | $1 \times 10^{6}$ | 0.065 | 0 |
| 65 d - 1 yr | 65,000 | 0.160 | 0 |
| 2 - 4 yr | 10,000 | 0.400 | 0 |
| 5 - 7 yr | 4,000 | 0.680 | 0 |
| 8 - 10 yr | 2,500 | 0.690 | 4,843,000 |
| 11 - 13 yr | 1000 | 0.700 | 5,960,000 |
| 14 - 16 yr | 700 | 0.710 | 7,078,000 |
| 17 - 19 yr | 600 | 0.720 | 8,195,000 |
| 20 - 22 yr | 500 | 0.730 | 9,313,000 |
| 23 - 25 yr | 450 | 0.740 | 10,431,000 |
| 26 - 28 yr | 400 | 0.745 | 11,548,000 |
| 29 - 31 yr | 350 | 0.750 | 12,666,000 |
| 32 - 34 yr | 300 | 0.755 | 13,783,000 |
| 35 - 37 yr | 250 | 0.760 | 14,901,000 |
| 38 - 40 yr | 200 | 0.765 | 16,019,000 |
| 41 - 43 yr | 100 | 0.770 | 17,136,000 |
| 44 - 46 yr | 50 | 0 | 18,254.000 |

2. Baseline + density dependence (Beverton-Holt, rho= $1 \times 10^{-14}$, k= 1.9)
3. Baseline + stock 250,000 "early" juvenile (30 - 65 d) fish
4. Baseline + density dependence + stock 250,000 early juveniles
5. Baseline + stock 25,000 "late" juvenile (65d - 1 yr) fish
6. Baseline + density dependence + stock 25,000 late juveniles
7. Baseline + double larval (0-30 d) survival rate
8. Baseline + double early juvenile survival rate
9. Baseline + double late juvenile survival rate
10 -18. Each of the above repeated + demographic stochasticity for larval survival rate (CV= 2.5, normal distribution)

Supplemental stocking of early and late juveniles was simulated using the migration option of RAMAS-Age. We performed two manipulations: addition of 2.5 x $10^5$ early juveniles (a quarter of the initial baseline abundance of this cohort), and addition of 2.5 x $10^4$ late juveniles (greater than a third of the initial baseline abundance of the cohort). By default RAMAS creates a minor random component during each time step, which yields variation around the mean of multiple runs with identical input data. We ran each simulated scenario 100 times for a period of 50 years. We then examined the mean abundance of the total population (minus the larval stage) after the final time step. To indicate responses by a typical adult cohort, we also examined mean abundance of the 20-22 yr class (near the middle of the range of age intervals). Mean abundance from each scenario was compared with the mean abundance from the baseline configuration. The magnitude of difference was expressed in terms of both absolute abundance and relative abundance (% change).

## Simulation Results

The baseline configuration yielded a slight decline in population abundance after 50 years (lambda = 1.0009). Imposition of density dependence decreased both the total population (Table 2) and the age 20-22 class (referred to hereafter as "age-20 fish") by 48% (Table 3).

Table 2. Summary of the response of the total population (including all age classes except larvae) from 18 simulated scenarios. Mean abundance is based on 100 simulations and a time span of 50 years.

| Model | Mean abundance | Percent change |
|---|---|---|
| 1. Baseline | 1.50 x $10^7$ | |
| 2. Density dependence | 7.73 x $10^6$ | –48% |
| 3. Stock early juveniles | 1.88 x $10^7$ | +25% |
| 4. Density-dep. + stock early juvs. | 5.70 x $10^6$ | –62% |
| 5. Stock late juveniles | 1.77 x $10^7$ | +18% |
| 6. Density-dep. + stock late juvs. | 8.29 x $10^6$ | –44% |
| 7. 2X larval survival rate | 3.63 x $10^9$ | +24,100% |
| 8. 2X early juvenile survival rate | 2.15 x $10^9$ | +1,420,000% |
| 9. 2X late juvenile survival rate | 2.13 x $10^{11}$ | +1,419,900% |
| 10. Baseline + stochastic larval survival | 1.18 x $10^4$ | –99% |
| 11. Stochastic + density dependence | 6.51 x $10^3$ | –99% |

Table 2 cont.

| | | |
|---|---|---|
| 12. Stochastic + stock early juveniles | $2.60 \times 10^4$ | –98% |
| 13. Stoch. + den. dep. + stock early juvs. | $1.60 \times 10^4$ | –98% |
| 14. Stochastic + stock late juveniles | $1.30 \times 10^6$ | –99% |
| 15. Stoch. + den. dep. + stock late juvs. | $1.30 \times 10^6$ | –99% |
| 16. Stochastic + 2X larval survival | $3.91 \times 10^4$ | –99% |
| 17. Stochastic + 2X early juv. survival | $1.55 \times 10^4$ | –99% |
| 18. Stochastic + 2X late juv. survival | $1.41 \times 10^4$ | –99% |

Table 3. Summary of the response of the 20 - 22 yr age class from 18 simulated scenarios. Mean abundance is based on 100 simulations and a time span of 50 years.

| Model | Mean abundance | Percent change |
|---|---|---|
| 1. Baseline | $8.95 \times 10^3$ | |
| 2. Density dependence | $4.64 \times 10^3$ | –48% |
| 3. Stock early juveniles | $9.05 \times 10^3$ | +1% |
| 4. Density-dep. + stock early juvs. | $5.84 \times 10^3$ | –35% |
| 5. Stock late juveniles | $9.63 \times 10^3$ | +8% |
| 6. Density-dep. + stock late juvs. | $8.70 \times 10^3$ | –3% |
| 7. 2X larval survival rate | $5.83 \times 10^5$ | +6,414% |
| 8. 2X early juvenile survival rate | $5.84 \times 10^5$ | +6,425% |
| 9. 2X late juvenile survival rate | $7.70 \times 10^7$ | +860,235% |
| 10. Baseline + stochastic larval survival | $8.66 \times 10^0$ | –99% |
| 11. Stochastic + density dependence | $3.92 \times 10^0$ | –99% |
| 12. Stochastic + stock early juveniles | $1.75 \times 10^2$ | –98% |
| 13. Stoch. + den. dep. + stock early juvs. | $1.74 \times 10^2$ | –98% |
| 14. Stochastic + stock late juveniles | $2.70 \times 10^2$ | –97% |
| 15. Stoch. + den. dep. + stock late juvs. | $2.68 \times 10^2$ | –97% |
| 16. Stochastic + 2X larval survival | $1.31 \times 10^1$ | –99% |
| 17. Stochastic + 2X early juv. survival | $2.04 \times 10^1$ | –99% |
| 18. Stochastic + 2X late juv. survival | $1.78 \times 10^1$ | –99% |

Density dependence tended to have a stronger influence on population dynamics than massive supplemental stocking of early juveniles (1 - 30 d). Supplemental stocking of early juveniles without density dependence resulted in a 25% increase in total abundance and a 1% increase in age-20 fish relative to baseline. The combination of density dependence and stocking of early juveniles yielded a 62% decrease in the total population and a 35% decrease in the abundance of age 20 fish relative to baseline.

Relative to density dependence without stocking, stocking of early juveniles with density dependence decreased the total population by 26% and increased age-20 abundance by 25%.

Supplemental stocking of late juveniles (30 - 65 d) caused an 18% increase in the total population and an 8% increase in age-20 fish relative to baseline. In contrast, stocking of late juvenile fish with density dependence resulted in a 45% decrease in total abundance and a 3% decrease in abundance of age-20 fish relative to baseline. Relative to density dependence without stocking, stocking of late juveniles with density dependence increased the total population by 7% and increased age-20 abundance by 87%.

The forcing of stochastic dynamics on larval survivorship on the baseline scenario caused a 99% decline in the total population and abundance of age-20 fish. Similar results were obtained when the stochastic feature was combined with density dependence, stocking without density dependence, and stocking with density dependence (Table 2, 3). Apparently, our seemingly modest stochastic adjustments of the baseline larval survival rate resulted in numerous simulations in which early recruitment was insufficient to sustain the population (population crashes) and infrequent cases in which early recruitment was enhanced to a degree sufficient to sustain or enhance the overall population.

To estimate the potential effects of early life stage recruitment under favorable environmental conditions or habitat restoration, we simulated the effect of enhanced survival rates for larval, early juvenile, and late juvenile fishes. The effect of doubling our empirical estimates of survival rates on population abundance was several orders of magnitude larger than any of the other simulated components (Table 2, 3). Given the very large numbers of eggs produced by the adult population each year, seemingly minor increases in survival rates of early life stages can have profound positive influence on tarpon populations.

## DISCUSSION

Detailed descriptions of tarpon population structure are lacking, but ample evidence indicates that fishes with periodic-type life histories (delayed maturation, high fecundity, long lifespan) experience large inter-annual variation in recruitment. During most years, survivorship of early life stages probably approaches zero in these populations. Only under particular environmental circumstances is above-average recruitment realized. These boom and bust recruitment dynamics imply high population variance in reproductive success within and between years. Density-dependent factors probably affect the survival and growth of early life stages only during infrequent years with exceptionally high recruitment. During normal years with poor to average recruitment,

density dependence is probably very weak or absent. Depending on key abiotic driving variables and species interactions, strong year classes could be affected by density-dependent processes over variable periods and regions. What are the implications of this life history strategy and mode of population regulation for the success of supplemental stocking programs for tarpon and other periodic-type fishes?

According to our tarpon model simulations, density dependence and stochastic variation in early recruitment have much greater influence on population abundance than massive supplemental stockings of juvenile fishes. As expected, stocking older fish had a greater per-capita effect on the population (the number of late juveniles stocked was 1/10 the number of early juveniles). However, the costs associated with rearing and releasing the massive numbers of late juvenile fishes required to enhance the population would likely be prohibitive. Large gains from stocking under the density-independent scenario were eliminated by the addition of weak density dependence. The addition of stochastic larval survivorship (simulating stochastic recruitment to age-1) completely eliminated the positive influence of age-1 stocking. Climatic and oceanographic conditions are probably the most important driving variables for early life stage success. Because environmental conditions responsible for early life stage survival are essentially unpredictable, there is little chance that the overriding influence of environmental stochasticity on the magnitude of stocking effect can be ameliorated.

Of course, simulation models cannot be expected to provide accurate and precise predictions of population dynamics. Instead, models allow us to examine relationships among key variables that influence dynamics. Our discussion of life history theory and our model simulations reveal some critical aspects of tarpon ecology that require careful consideration before initiating a supplemental stocking program in Texas or other locations. Clearly, the degree to which natural recruitment to juvenile age classes is influenced by stochastic factors needs to be evaluated carefully. If stochastic abiotic factors indeed strongly influence recruitment, then supplemental stocking should have negligible influence on long-term population trends. Likewise, density dependence has the potential to negate any positive influence of supplemental stocking. We simulated strong density dependence and large supplementations of young fish to the natural population. For most periodic fish species, including tarpon, we have little or no knowledge of the degree that density-dependent mechanisms, such as food limitation or predation, influence recruitment dynamics (Rose et al. 2001). Clearly, if density dependence is significant, it is highly variable in time and space. To detect and quantify this variation remains one of the greatest challenges of fisheries management.

Tarpon spawn offshore and, following variable periods in marine pelagic waters, metamorphosing larvae migrate or are transported through coastal passes and reside in

coastal marshes (Crabtree et al. 1992, Crabtee 1995). Shenker et al. (1995, this volume) documented episodic strong recruitment into the Indian River Lagoon, Florida in association with a tropical depression. Apparently, the storm altered coastal currents in a manner that increased entry of larval tarpon into this coastal system. These kinds of unpredictable, large-scale events are believed to influence early life stage recruitment in marine fish populations (Rothschild 1986). In addition, stochastic abiotic factors can interact with biotic factors (e.g., food supply and predator densities) to influence recruitment dynamics of early life stages (Bailey and Houde 1989). Recently, Fromentin et al. (2001) analyzed 136 long-term time series of juvenile cod (11 populations) and found that population variability was a function of both density-dependent processes and the interaction between density-dependent processes and stochastic factors.

Scharf (2000) determined that periodic appearances of strong year classes of red drum (*Sciaenops ocellatus*) were positively correlated across estuaries in Texas, which suggested that factors determining distribution and abundance in this species vary on large spatial scales. Correlative evidence suggested density-dependent mechanisms influenced age-0 survival of red drum, and juvenile survival appeared to influence year-class strength. These patterns are consistent with predications about population regulation in periodic strategists, and the red drum certainly possesses all of the attributes of the periodic strategy. Scharf was unable to detect any effects from a decade of supplemental stocking of hatchery-reared juveniles on the abundance of age-0 and age-1 red drum in Texas. This finding is consistent with our theoretical arguments and predictions based on results from our model simulations.

By far, the greatest effect on our simulated population dynamics (100 to10,000-fold increase relative to baseline) was created by doubling the survival rates of early life stages. Smaller increases in survival rates of naturally produced larvae yielded similar positive effects. For example, a chronic increase in larval survival of just 1% increases age-20 abundance by 1.000% (tenfold) over baseline. Fisheries management is largely powerless to influence larval survival rates. However, a variety of management actions can potentially influence survival rates of juvenile life stages of tarpon. Juvenile tarpon inhabit freshwater and brackish coastal marshes. On Florida's east coast, water control structures often block the entrance of fishes and macroinvertebrates into coastal marshes and disrupt normal hydrodynamics (Lin and Beal 1995). These wetlands are essential habitat for young tarpon (Crabtree et al. 1997, Shenker et al 1995). Reduction of freshwater discharge to coastal habitats alters hydrology, salinity regimes, and system productivity, all to the detriment of juvenile fishes that exploit secondary production in these productive ecosystems. Actions that enhance or restore access to and the quantity and quality of essential juvenile habitat have far greater potential to enhance tarpon

populations than supplemental stocking programs. A mere 1% increase in late juvenile survival increases age-20 abundance by 2,224% (more than tenfold) over baseline.

We conclude that supplemental stocking, even on a massive scale, is unlikely to have a major effect on tarpon and other coastal marine fish populations with periodic life-history strategies. Tarpon year classes are expected to be highly variable and strongly influenced by stochastic factors operating on broad spatial scales. Density-dependent processes probably influence early growth and survival under appropriate conditions during unusual years. Periodic strategists also are vulnerable to overfishing from which their populations recover slowly due to their advanced maturation age and unpredictable recruitment dynamics (Adams 1980). Given the great natural potential for high recruitment under appropriate conditions, it seems unlikely that supplemental stocking with hatchery-reared fish can significantly impact tarpon stocks. The great mobility of tarpon (with potential for Gulf-wide movement) and regionally variable fishing mortality also make stocking programs risky investments. More ecological research and demographic analysis is needed before large investments are made in support of research on captive rearing and hatchery production. A more viable strategy for tarpon population enhancement would be to protect wild breeding stocks (as is being done currently in Florida and Texas) coupled with watershed and coastal habitat management to improve juvenile tarpon access to productive marsh habitats essential for their feeding, growth, and survival.

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# TARPON: TOURISM RESOURCE OF THE GULF OF MEXICO

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## Historic tarpon distribution and abundance off the coast of Mexico

Tarpon once were abundant in the Mexican rivers that flow into the Gulf of Mexico. The Panuco, Tuxpan, Tecolutla, Coatzacoalcos, Palizada, and the Rio Grande rivers had tarpon present for several months off their mouths. During the 1960's tarpon numbers began to decline as well a number of other associated species such as members of the family Carangidae.

## Tarpon utilization as a fishery resource

Mexican laws extend protection to tarpon and allow the fishery only in a 50 km zone adjacent to the coast. By law, tarpon is reserved exclusively for the sport fishery. However implementation of conservation laws is difficult due to lack of resources and tarpon are commercially exploited for local and foreign markets (human consumption, fish meal, roe, and scales for exportation) in areas where law enforcement by the Federal Government is limited. It is possible that in the future law enforcement responsibilities will be under state government jurisdiction to facilitate application of the law and therefore the protection of the resource.

## Tarpon research in Mexico

Research on tarpon is very limited because this species is not considered a typical commercial species. Research efforts are concentrated on species of commercial value.

## Tarpon as ecotourism attraction

The abundance of tarpon in Mexican waters stimulated the organization of several international tarpon sport fishery tournaments. The first tournament was held in 1942 in Tampico. In 1946 the first tournament off Veracruz was organized. Later Tuxpan, Tecolutla, Coatzacoalcos and Ciudad del Carmen added tournaments. During the 1950's the Mexican government developed plans to utilize the historic, cultural, and natural resources of Mexico to encourage tourism as an industry. The recreational fishery was considered an important component of this plan to be marketed as a first class product to be promoted as a tourism attraction with potential to impact the Mexican economy. In the case of tarpon, several world record fish have been caught in the Panuco River. However, lack of scientific information to predict the tarpon migration along the Mexican coast, and almost nonexistent data on the status of the resource, prevent the full utilization of tarpon as a tourism attraction in Mexico.

## SUMMARY

Tarpon have declined in Mexico's Gulf waters since the 1960s. Despite laws limiting recreational harvest and proscribing commercial harvest, tarpon have not recovered to previous numbers observed in Mexican waters. The value of tarpon as a tourist attraction holds hope that effective protection will be brought to bear, reestablishing tarpon as a premier sport fish on the Mexican Gulf coast. I suggest that gatherings such as this first International Tarpon Symposium serve a valuable function in summarizing what's known of tarpon and proposing international cooperative research and conservation. I believe that it is especially important to coordinate research efforts on phenomena such as migration. Tournament fishermen, such as those I represent, are an important source of knowledge concerning tarpon ecology, behavior, and distribution, and should be involved in these research efforts. Tournament fishermen must become involved in the conservation effort by limiting the impact of tournament catches on this resource, perhaps by limiting retention to the three largest fish caught.


# CULTURE OF LEPTHOCEPHALI AND JUVENILES OF TARPON (*MEGALOPS ATLANTICUS*) COLLECTED FROM WILD STOCKS OFF THE CARIBBEAN COAST OF COLOMBIA


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## INTRODUCTION

Tarpon is a euryhaline species with the ability to adapt to a wide range of salinities and to tolerate low levels of dissolved oxygen. These adaptations facilitate the wide distribution of this species under a diverse range of environmental conditions. In Colombia, tarpon juveniles and leptocephali larvae are found in mangroves, lagoons, creeks, sea drainages, and inlets. Tarpon leptocephali are most abundant on the Colombian coast during the rainy season (April to December), but occur over most of the year which may indicate multiple spawning.

Tarpon are valued in Colombia's marine waters for sport and as a valuable source of protein. The ability to survive and prosper in brackish and freshwater make tarpon a prime candidate for stocking in a wide range of conditions. In addition to the increased opportunity to utilize tarpon as a sportfish and food source, stocked tarpon also may act as a control on nuisance species such as tilapia. The large size and voracious appetite of

tarpon may facilitate reductions in population density of this and other introduced fish species.

Preliminary research trials at our facility showed tarpon to have adequate densities of larvae and juveniles in Colombian waters to supply the numbers needed for extensive aquaculture. Similar conditions may exist in the Caribbean, South America, and Africa, opening opportunities in these regions for government and other entities to duplicate our efforts. In this abstract I describe the methods we utilized to capture, culture, and stock tarpon in Colombian Caribbean inland waters.

## Tarpon collection and maintenance

Larvae were collected on the Caribbean side of Cartagena in depths of about 40 cm, at temperatures as high as 39° C with an average temperature of 31°C. These collection sites were often characterized by high levels of sulfates, low pH, and near anaerobic water. Larvae were generally captured using dark fine-mesh dip nets made of cotton treads to reduce damage to the fragile larvae. These larvae were feeding on zooplankton; dissected larvae contained mosquito larvae as a predominant prey item. A group of larvae was maintained in aquaria in order to observe and describe metamorphosis (Mercado 1969, 1972). These larvae were fed *Artemia nauplii*, copepods, and mosquito larvae and were kept until metamorphosis into early juveniles (Mercado 1971). Juveniles were captured using cast nets and seines made of cotton. Captured juveniles range in size from 80-350 mm TL, with the most abundant size class being 150-250 mm TL. To avoid intraspecific competition, larvae and juveniles tarpon were sorted by size prior to being placed in pens where they were held for 3 to 4 days with cages placed in deeper water.

Following this period the young tarpon were dipped from pens using a dark fine-mesh dip net, placed in plastic bags filled with approximately 10 liters of water with 60-80 larvae/liter, then transported by automobile or boat to stocking sites which included coastal lagoons connected to the sea, man-made earthen ponds connected to estuaries and mangrove swamps, and a variety of freshwater habitats. At the stocking site the young tarpon were held in pens with densities ranging from 3,000-5,000 individuals/$m^3$. After completion of metamorphosis the densities in the cages were reduced to 1,500-2,000/$m^3$. Fingerlings were maintained under these conditions for 3-4 months prior to stocking. A variety of foods were used to maintain the juvenile tarpon, including extruded pellets with high protein content, trash fish, cattle and poultry industry by products, cassava, and cooked rice. Mortality during this period was less than 10%. Most of the mortality was attributed to stress related to capture and transportation of leptocephali.

We experimented with both extensive and semi-intensive culture and both monoculture and in polyculture. Species maintained with tarpon included members of the family Mugilidae, Centropomidae, Carangidae, Gerridae, and Ariidae.

## Stocking

Tarpon produced in these studies have been stocked into fresh, brackish, and saltwater. Tarpon juveniles from monoculture experiments were stocked at approximately the same size to avoid cannibalism. Tarpon from mixed-species experiments were stocked along with the other species cultured and at different sizes.

Lakes stocked for sport and subsistence fisheries included Laruaco Lagoon, El Totumo Lagoon, El Cisne Lagoon, Tocaagua, and Las Ventas. As an example of the success of these stocking efforts the stockings at Laruaco Lagoon are informative. This 420 ha body of water was stocked with 6,700 tarpon averaging 431 mm TL. Six years later the lagoon was utilized by an artisinal-commercial fishery for four months and a six day recreational tournament was held. A total of 6,050 tarpon were recovered. The average weight of these individuals was found to be 11 kg and length varied from 1,000-1,500 mm TL. Other species associated with tarpon in Laruaco Lagoon were *Hoplias malabaricus, Caquetasia krausii, Aequidens pulcher, Roboides dayi dayi, Symbranchus marmoratus, and Astianax* spp.

## Tarpon grow-out

Some tarpon were maintained over extended periods in 100$m^2$ pens or in earthen ponds ranging from 30-3,000 $m^2$ which were connected to lagoons or lakes by gravity drainage or pumped through pipelines. These ponds were stocked at initial densities of 3 fish/ha, 10,000/ha, 30,000/ha, and 50,000/ha and supplemental feed was provided consisting of trash fish and chicken guts. Juveniles under 50 mm TL were fed floating pellets.

We closely examined one experimental condition in which tarpon were stocked in ponds at approximately 200 mm TL at densities of 1 fish/30$m^2$, then fed with cut trash fish. Nine months later the pond was sampled and the fish were found to average 690 mm TL and 3.0 kg of weight. After 15 months the average length increased to 830 mm TL with an average weight of approximately 6.0 kg.

## Tilapia control

Tarpon were stocked into 6,000 $m^2$ ponds at a density of 0.03 tarpon per $m^2$, with individuals of approximately 225 mm TL and 72 g. The ponds had resident populations of *Tilapia rendalii* which averaged approximately 100 mm TL. After 13 months all tarpon were recovered and were found to average 825 mm TL with weights averaging 6.0 kg. Tilapia recovered during the same period were larger individuals which had escaped tarpon predation.

## SUMMARY

During the period of 1969-1990 the National Institute of Natural Resources (INDERENA) in Cartagena, Colombia collected leptocephali and juveniles of wild tarpon (*Megalops atlanticus*) off the Colombian Caribbean coast. These individuals were

maintained in captivity until they were of adequate size to stock into inland waters. The purposes of collecting, culturing, and stocking tarpon were to 1) increase fishing opportunities for sport-fishermen and the general public, and 2) to act as a biological control on pernicious fish species considered pests in Colombian inland waters. Culture of tarpon required acquisition of massive numbers of leptocephali and early-stage juveniles which were held in cages and pens located in lagoons and other inland bodies of water. This allowed the leptocephali to metamorphose and the young tarpon to grow large enough to escape most predation and increase their probability of survival. During this period the young fish were offered supplemental feed.

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## RADIOMETRIC AGE VALIDATION OF THE ATLANTIC TARPON, *MEGALOPS ATLANTICUS**

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An improved radiometric ageing technique was used to examine annulus-derived age estimates from otoliths of the Atlantic tarpon, *Megalops atlanticus*. Whole otoliths from juvenile fish and otolith cores, representing the first 2 years of growth, from adult fish were used to determine $^{210}Pb$ and $^{226}Ra$ activity; six age groups consisting of pooled otoliths and nine individual otolith cores were aged. This unprecedented use of individual otolith cores to determine age was possible because of improvements made to the $^{226}Ra$ determination technique. The disequilibria of $^{210}Pb$:$^{226}Ra$ for these samples were used to determine radiometric age. Annulus-derived age estimates did not agree closely with radiometric age determinations. In most cases, the precision (CV ≤ 12%) among the otolith readings could not explain the differences. The greatest radiometric age was 78.0 yr for a 2045 mm FL female, where the radiometric error encompassed the annulus-derived age estimate of 55 yr by about 4 yr. The greatest radiometric age for males was 41.0 yr for a 1588 mm FL tarpon, where the radiometric error encompassed the annulus-derived age estimate of 32 yr by 1 yr. Radiometric age determinations in this study indicated that the interpretation of growth zones in Atlantic tarpon otoliths can be difficult, and in some cases may be inaccurate. This study provides conclusive evidence that the longevity of the Atlantic tarpon is greater than 50 years.

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## EARLY LIFE HISTORY OF THE ATLANTIC TARPON, *MEGALOPS ATLANTICUS*, ALONG THE UPPER TEXAS COAST

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The Atlantic tarpon, *Megalops atlanticus*, is one of the most prized sportfish in Gulf of Mexico, southeastern Atlantic, and Caribbean coastal waters. Unlike other popular sportfish, i.e. spotted seatrout and red drum, little is known about early life history,

biology, and ecology, which are essential for conservation and management strategies. To date, all existing information has been collected from Florida, the Caribbean, and South America, while only anecdotal information has been gathered in the northwestern Gulf of Mexico. The objectives of this research were to assess the abundance and distribution of juvenile tarpon along the upper Texas coast, from Galveston Bay to Corpus Christi Bay, and identify habitat and hydrographic preferences. Over a hundred sites were sampled with bag seines and cast nets during July-November, 1992-93, and ten sites were monitored on a monthly basis to determine recruitment, growth, and retention information. Ninety-two juvenile tarpon (17-206 mm SL) were captured during the study period, eight of which were recaptures. Juvenile abundance was highest in August and catches were minimal in September, October, and November. Nearly all tarpon were captured in marsh habitat with limited tidal exchange to open water. Captures occurred in salinities ranging from 21 - 35 ppt; water temperatures 16 - 31 C; and, dissolved oxygen content 1 - 9 mg/l. Results from this research suggest that juvenile tarpon exhibit episodic recruitment into northern Texas estuaries and temporarily reside in shallow, tidally restricted marsh habitats. Survival of juveniles in these habitats is unknown but we speculate that it is low due to bird predation and timing of tidal flushing. Since captures were limited, we provide a descriptive assessment of habitat use, growth, and movement within Texas estuaries.

## A REVIEW OF RECENT TARPON RESEARCH ACTIVITIES: WHAT IS KNOWN AND WHAT IS NOT?

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Tarpon research dates back to the turn of the century, but the first significant contributions were made in the 1940's. These early studies focused on identifying life history stages and describing habitat, but they also included some of the first attempts at ageing tarpon with scales and described spawning seasonality. Papers were also published between 1960 and 1980 reporting on the distribution of tarpon larvae and the possible location of spawning areas. With the advent of Sportfish Restoration funds in the late 1980's, and the development of more restrictive management of tarpon in Florida in 1989, funding for tarpon research became available. Research in Florida during the 1990's addressed many aspects of tarpon biology. These studies addressed age and growth, radiometric ageing, reproduction, early life history, recruitment, air-breathing

physiology, and population genetics. Although much progress has been made, questions remain regarding many aspects of tarpon biology. Little is known about spawning areas and behavior. Fertilized eggs remain undescribed. No estimates of batch fecundity or spawning frequency exist and few, if any, fully hydrated ovaries have been seen. Growth rates of larvae during the metamorphic period are poorly known and few metamorphic larvae and small post-metamorphic juveniles have been collected. Age and size at sexually maturity is poorly known. Due to the difficulties in using otoliths to age tarpon, questions remain regarding growth and mortality. No estimates of tarpon population size exist and migratory patterns are known only in a general way. Current recreational surveys are inadequate to derive meaningful estimates of the total catch or catch rates, which could be a useful index of tarpon abundance. The catch-and-release nature of the tarpon fishery, and the limited supply of specimens for study make progress on many issues difficult.

## AGE, GROWTH AND REPRODUCTION OF TARPON IN PUERTO RICO

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The purpose of this study is to present age and reproductive information of tarpon in Puerto Rico in order to set the baseline data required to properly manage this valuable sportfishing resource. For this objective, the combined effort of acquiring 50 samples per month from commercial fisherman supplemented by experimental sampling with trammel and gillnets in three Puerto Rican estuaries was done from May 1992 to December 1995. Annual growth marks in tarpon otoliths were validated by Mark and Recapture experiments and marginal increment analysis showed that annuli formed between April and June. The growth rate of recaptured fish (n =3) ranged from 0.09 to 0.26 mm/day. The average estimated growth rate for male tarpon (n= 105) was 1.04 mm/day and for females (n = 110) 0.72 mm/day. The oldest male and female tarpon found was 10 years and 21 years old respectively. Female were larger than males with the maximum observed size for male tarpon at 1020 mm Fl and for females 1740 mm Fl. Size and ages at 50% maturity for male and female tarpon were 785 mm Fl (age 5) and 850 mm FL (age 5-6) respectively. The spawning season was estimate to last from April to early august with batch fecundity ranging from 127935 to 8,402,788 oocytes. Spawning frequency average one spawn per every 30 days and distance from shore to spawning grounds was estimated at about 2 km. Tarpon life history characteristics, slow

growth and longevity are typical of fish prone to overexploitation. The historical records in Puerto Rico from Commercial and sportfishermen landings indicate a decrease in sizes which may be indicative of stock reduction.

## HISTORICAL OVERVIEW OF TARPON IN TEXAS

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Prior to the 1950s, Texas was home to a recreationally important tarpon fishery. As early as the 1880s, bountiful tarpon assemblages attracted fishermen to Port Aransas, then known as Tarpon. Gulf waters off Port Aransas and Aransas Pass alone accounted for nearly 8300 tarpon landings during 1903-1910. Other tarpon "hotspots" including Galveston, Corpus Christi, and Port Isabel had drawn the acclaim of naturalists and fishermen alike by the 1920s. Port Aransas held the title of "Tarpon Capital of the World" from the 1920-40s and, in so doing, attracted notables such as Franklin D. Roosevelt in search of the silver king. Despite this historical abundance, Texas' recreational tarpon fishery has been virtually nonexistent for the last 50 years. The perceived post-1950 demise of Texas' tarpon stocks is a frequently debated subject without a consensus as to possible cause(s). To this end, published and unpublished literature, interviews with guides and fishermen, and limited scientific data are used to trace historical trends in spatial and temporal occurrence of tarpon in Texas' recreational fishery. Angling patterns and anecdotal information on landings provide historical insight into population dynamics of subadult through adult tarpon along the Texas coast. Field data collected by the Texas Parks and Wildlife Department and Texas A&M University at Galveston are summarized to describe the occurrence of immature tarpon and their dependence on Texas waters. Theories as to the source(s) of tarpon (resident versus transient stocks) historically captured in the recreational fishery and factors promoting their use of state waters are reviewed. Human-related and environmental factors possibly influencing the suspected demise of tarpon in Texas also are considered. An overview of TPWD's historical and current stock assessment efforts, management strategies, and recovery initiatives for tarpon also is presented.

## THE CHALLENGES OF SPAWNING TARPON IN CAPTIVITY

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Captive spawning has been used successfully to produce juvenile fish for restocking depleted natural populations, most notably in Texas for red drum. Captive spawning may contribute to a comprehensive effort to enhance tarpon stocks in Texas through the provision of fertilized eggs for research and eventual release. However, several aspects of tarpon biology present significant challenges to the development of captive spawning protocols. Dependable sources of broodstock must be identified. Facilities for large, pelagic fish must be established in which tarpon can be held under controlled conditions that promote growth and reproductive development. Techniques must be developed for noninvasive determination of sex and reproductive condition in both adults and juveniles. Finally, technologies must be applied that result in predictable production of fertilizable gametes and spawning behavior in captivity. Sea Center Texas has kept up to 9 adult and subadult tarpon for over three years. During this time, animals have been held on a simulated natural photoperiod and temperature cycle, increasing in weight over 175% on a diet of fish, squid, and shrimp. We have developed techniques for obtaining blood samples from both captive adults and juveniles in the field. We propose to use these resources to develop hormone based-techniques for sexing and determination of reproductive development of tarpon held in captivity. These techniques can be used to identify the optimal times for application of gonadotropin-releasing hormone implants to promote gamete release and spawning behavior. Whereas this may result in the first observation of a fertilized tarpon egg, successful captive breeding of tarpon will also depend on the development of a better understanding of the biology and rearing the tarpon's unusual leptocephalus larva. Additional research on the reproductive biology of both wild and captive tarpon is needed to facilitate these efforts.

## GEOGRAPHIC VARIATION IN MOLECULAR AND MORPHOMETRIC CHARACTERS OF TARPON (*MEGALOPS ATLANTICUS* VALENCIENNES) IN THE NORTH ATLANTIC OCEAN

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The tarpon (*Megalops atlanticus*) is a highly valued game fish and occasional food fish in the eastern and western Atlantic Ocean. In this study we used three genetic techniques - protein electrophoresis, mitochondrial DNA (mtDNA) restriction fragment length polymorphism (RFLP) analysis, and mtDNA sequence analysis - to assess this species' population structure in the northern and equatorial Atlantic. These analyses demonstrated that, within the range of our study, the population structure of this species varies over range-wide and regional scales. Genetic divergence was evident between tarpon from Africa and tarpon from the western Atlantic Ocean. Significant differences in allele and haplotype frequencies and isolation by distance between the African and western Atlantic samples indicated that tarpon from these regions currently share little or no gene flow. In addition, the low genetic variability of the African sample may have resulted from a recent founder event or population bottleneck or by prolonged or recurrent episodes of reduced population size, possibly due to historic environmental variation. Among the western Atlantic Ocean collections, genetic variability estimates and allele and haplotype frequencies were similar; isolation by distance was low; and migration values were high. Nevertheless, there was evidence of subtle population structuring. A clade of mtDNA RFLP haplotypes found only in Florida differed significantly from all other haplotypes. Also, the basal position in allozyme and mtDNA-sequence phenograms of tarpon in the Costa Rican collection suggested that gene flow is comparatively low between the tarpon of Costa Rica and tarpon of other western Atlantic locations. Ultimately, international cooperation will be essential in the management of this species in both the eastern and western Atlantic Ocean.

## SPORT FISHING OF TARPON (*MEGALOPS ATLANTICUS*) ALONG THE MEXICAN COAST OF THE GULF OF MEXICO

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In Mexico, the tarpon fishery is regulated by law with captures reserved only for sport fisheries. In the Gulf of Mexico tarpon "Fishing Clubs" or associations of sport fishermen organize tournaments. In the state of Veracruz these associations are located in Tuxpan, Tecolutla, Veracruz, and Coatzacoalcos. Tournaments usually take place during summer time and coincide with the "runs" of tarpon in the Veracruz Coast. Tarpon in Veracruz is incidentally caught in the sharks and snook fishery since these organisms exhibit similar spatial distribution and/or share the same habitat during stages of their life cycle. Data on tournament catches and fishing techniques of sport fishermen in the Port of Veracruz, Veracruz, Mexico will be presented. Data on tarpon incidental catches by Veracruz small scale commercial and artisanal shark and snook fishery and their fishing arts utilized by Veracruz fishermen will be described. Difficulties faced in tarpon tag recovery programs will be explored and suggestions to expedite tag recovery through cooperation of governmental agencies including regional institutions (CRIP-Veracruz, INP, and SEMARNAP) with the common mission to manage and protect marine natural resources. The importance of utilization of data compiled on tarpon catches and fish lengths by the "fishing clubs" on the annual fishing tournaments will be highlighted and historical trends analyzed as well as the tags recovered during these tournaments.

## TARPON TAGGING IN THE GULF OF MEXICO

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Fish Trackers, Inc. is a non-profit organization researching movement and growth of various marine species in the Gulf of Mexico, Atlantic Ocean and Caribbean Sea. FTI supplies tags and equipment to anglers who cooperate in this effort by catching, tagging, releasing and recording release data on each fish and sending this information to FTI. Since 1985 when the program began, 78012 fish representing 132 species have been tagged and released with 10,658 recaptures. The tarpon is one of the 132 species tagged and released in FTI's tagging program. Not many tarpon have been tagged and far fewer have been recaptured. According to FTI records for the past 15 years, Florida has had the highest number of tarpon tagged recaptured, followed by Texas. Tagging a tarpon requires a little more effort than tagging other species because the fish is usually to large to easily handle and the tarpon's scales are large and sometimes difficult to penetrate with tagging equipment. There are several tagging organizations that include tarpon as one of the tagged species. Although recapture rates seem low, a major problem seems to be in non-reporting of recaptures by the angling community. There is a need for educating anglers on what to do with the tagged fish, tarpon or other species, when they recapture one.

# EFFECTS OF DEPTH AND PLANT COVER ON JUVENILE SPORTFISH DISTRIBUTION IN A PUERTO RICAN MUDFLAT: AN EXPERIMENTAL FIELD STUDY

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Preliminary sampling indicated the existence of juvenile fish aggregations in deeper areas of mudflats in Boquerón Bay, Puerto Rico. A series of eight artificial pools were constructed to test the effect water depth and plant cover have on the distribution and density of four sportfish species; *Megalops atlanticus* V., *Centropomus undecimalis* B., *Centropomus ensiferus* P. and *Elops saurus* L. The test area was characterized by high variations in salinity, temperature and strong avian predation. A total of 16,539 fish (34 species) were captured with *E. saurus* and *Oreochromis mossambica* being the most abundant fish species. Responses to pool depth and plant cover were found to be species specific, which was caused by behavioral differences and differences in microhabitat use. The choice of microhabitat may have important consequences on the survival of the species. Snook species were found to be associated with the pneumatohpore habitat while *E. saururs* preferred the non-vegetated mudflat. Temporal co-occurrence of recruitment occurred between species but different microhabitat use was observed. Stomach analyses demonstrated that the diet of *M. atlanticus* and *E. saurus* became diversified with ontogenetic changes. Created pools and natural pools showed similar habitat use and value. Although, plant cover mitigated changes in water temperature, pool depth failed to buffer environmental parameters; however, pool depth probably helped reduced avian predation. Consequently, plant cover and water depth have important effects on juvenile sport fish distribution.

# COOPERATION BETWEEN FISHERMEN, GUIDES, SCIENTISTS AND FISHERY MANAGERS

**Moderators: Andre Landry and Dave Sullivan**

## INTRODUCTION

Round table discussions by fishermen (7), guides (3), scientists (3 university researchers), and fishery managers (9 Texas Parks and Wildlife Department personnel) plus representatives of the Coastal Conservation Association and the International Women's Fishing Association identified issues, priority needs, and action plans related to enhancing tarpon stocks in Texas and the Gulf of Mexico. Discussions focused on the concern that tarpon stocks in Texas and Mexico have seemingly declined from those historically present through the mid-1960s and no one knows why. A summary of issues and needs most important in tarpon recovery efforts, along with recommendations to achieve them, are presented below.

## RESULTS

Discussion moderators proposed answering three questions as an initial approach to addressing the tarpon's plight in Texas and the western Gulf. These questions were:

1. What caused the historical Texas tarpon fishery's demise?
2. What can be done to recover the present fishery to historical levels?
3. What role can the recreational fishery, scientific community and regulatory agencies collaboratively play in this recovery?

With this charge, initial discussions revisited anecdotal information about the Texas tarpon fishery and factors influencing historical stocks. Most participants felt this information, especially that prior to the mid-1960s, generated more questions than answers. Participants did agree tarpon are a migratory stock that uses Texas waters on a seasonal basis, and any realistic attempt to rehabilitate this stock must involve collaboration between Texas, other Gulf States, and Mexico. The group then reexamined several issues stemming from the aforementioned anecdotal information to conclude: The key to understanding historical trends in the Texas tarpon fishery and promoting effective management and eventual recovery of present stocks rests on our ability to generate technical information on: 1) tarpon life history in Texas and other states/countries; and 2) the role environmental and human-related factors play in this species' use of Texas and western Gulf waters. Participants felt this information was essential to establishing more directed management strategies for tarpon in Texas and developing legislative support for politically sensitive initiatives designed to benefit tarpon habitat. With this in mind, participants prioritized specific research and extension goals that must be realized if

resource managers and legislators are to institute steps at the state, federal and international level to recover tarpon stocks Gulfwide. These research and extension goals are summarized below.

***Research/Extension Goal #1***

Characterization of tarpon life history in the western Gulf was assigned top priority in formulating recovery efforts for this species. To this end, participants recommended conducting life history studies that: 1) describe population dynamics of tarpon in the western Gulf, especially those life stages occurring in Texas and Mexican waters; 2) identify essential habitat in the western Gulf to which tarpon recruit; and 3) assess impact of the Gulf's recreational tarpon fishery and Mexico's commercial fishery on the overall health of tarpon stocks.

Four approaches were recommended in the conduct of tarpon life history studies. "High-tech" telemetry, such as that afforded by satellite and archival tags, was assigned the highest priority approach in determining movements and behavior of tarpon Gulf wide. This state-of-the-art technology was proposed as a "big bang for the buck" initiative for quickly generating essential information that traditional streamer and internal tagging efforts take years to produce. A collaborative satellite-tagging program incorporating fishermen, guides, and scientists across strategic tarpon fishing locales such as Boca Grande, FL, Empire-Venice, LA, Galveston-Port Aransas, TX and Tampico-Veracruz, Mexico was proposed as the most effective means of generating Gulfwide information on spatial/temporal movements, source of tarpon stocks migrating to western vs eastern Gulf habitats, habitat requirements, etc. Participants suggested tags be purchased by fishermen or fishing associations and donated to the collaborative tagging program. A second recommendation receiving high priority was the development of an effective network of guides, fishermen, and fishing industry representatives to serve as fishery ambassadors promoting recovery strategies for tarpon. Network constituents would function as "eyes on the water" in providing additional life history data/samples (i.e., scales for genetics, size, spatial/temporal occurrence) and educate the fishing public in correct ways to tag and release tarpon, pull scales, etc. Most participants felt tarpon guides and fishermen were a source of information that is not being used effectively to facilitate tarpon recovery. A third priority was assigned to conducting special monitoring studies generating data that fill particular information voids or address critical issues not effectively resolved by current coastal finfish surveys. Lastly, current monitoring programs conducted by state agencies to characterize tarpon dynamics should be continued but evaluated on the basis of location, timing and gear selectivity as to their ability to provide meaningful information on population status, size composition, spatial/temporal occurrence, and habitat preference in the western Gulf.

### *Research/Extension Goal #2*

The role freshwater inflow plays in tarpon life history and this species' use of Texas waters must be assessed in terms of its impact on habitat quality. However, no clear approach was agreed upon in assessing the influence of freshwater inflow on maintenance of essential tarpon habitat. Tracking dam construction's impact on historic tarpon assemblages in Texas and the need for legislatively mandated freshwater releases into estuarine environments used by tarpon life stages dominated discussion on this topic. Priority was given to determining the relationship of freshwater inflow in maintaining essential habitat used by tarpon for early life history survival strategies, nursery areas for young-of-the year and yearlings, and feeding grounds for juvenile through adult life stages.

### *Strategic plan*

Discussion participants recommended Tarpon Tomorrow integrate the aforementioned research and extension goals, along with those identified by other round table discussion groups, into a strategic plan for developing pertinent action items, subsequent proposals, and prerequisite funding. The tarpon's migratory nature will necessitate this plan seek funding from state, federal and international sources for research in the western Gulf addressing tarpon life history and freshwater inflow's impact on this species' dynamics. With few exceptions, this research will generate the first scientifically documented information on tarpon stocks in the western Gulf. This information is essential to attaining two tarpon recovery products: 1) a near-term evaluation and possible revision of current fisheries monitoring programs and fishing regulations designed to yield more responsive management strategies and up-to-date information on all tarpon population constituents; and 2) development of long-term data bases upon which to obtain legislative support for passing politically-sensitive regulations protecting and enhancing essential tarpon habitat.

## MANAGEMENT OF TARPON THROUGHOUT THE DISTRIBUTION OF THE SPECIES

**Moderator: Bob Colura**

Twelve fisheries scientists and one recreational angler/conservationist attended the round table discussion of tarpon management. Panel members were Dr. Refugio Castro, Mr. Mario Cruz Ayala, and Dr. Kirk Winemiller. The discussion centered on current management practices primarily in the Gulf of Mexico. It was agreed that current

management strategies are, for the most part, conservative but improvement of management strategies are hampered by lack of data. A summary of the discussion of management practices and problems in Mexico and the United States follows.

### *Mexico*

Tarpon in Mexico are managed as recreational fish by the federal government. Tarpon may only be retained and sold if they are bycatch from the commercial fishery. About 400,000 families are dependant on fishing for their livelihood; therefore, Federal fisheries research and management programs are directed toward commercial fisheries. Sport fishing has a smaller impact on the economy but is growing and a Gulf Tourism Program is pushing for more research into tarpon management.

No fishery independent data are collected for tarpon management. Data for tarpon management is obtained from tournaments. Harvest of tarpon is permitted only during tournaments. Tournaments are authorized and permitted by the federal government but regulations concerning size and harvest are established by each state. Each angler in a tournament is required to have a permit. Data does not indicate tarpon are declining though antidotal evidence suggests a decline has occurred on the Gulf coast. In the 1960's tournament entries of about 250 people would land about 200 tarpon. Currently tournament entries of 600 people catch only four or five tarpon. No decline has been noticed on the Caribbean coast.

### *United States*

Tarpon in the United States are managed as a recreational fish with individual states regulating the fishery within their jurisdiction. No regulations on tarpon are in effect in waters under federal jurisdiction. Florida tarpon populations appear to be the most stable and allow a two fish daily possession limit with the purchase of a tarpon tag. Alabama has a 60 inches (152.4 cm) total length minimum size limit and requires the purchase of a tarpon tag to harvest a tarpon. In Texas one tarpon 80 inches (203.2 cm) total length minimum size may be harvested annually with the purchase of a tarpon tag. Louisiana and Mississippi have no regulations. Antidotal information suggests tarpon populations are not currently as large as populations 50 or more years ago. This appears to be especially true in Texas.

Both fishery dependent and independent data are collected in the U. S. though only Florida tarpon populations are large enough to allow the collection of a significant amount of data. Texas data is generally confined to samples from juvenile and sub-adult tarpon populations.

# CURRENT STATUS OF TARPON RESEARCH AND FUTURE TARPON RESEARCH OPPORTUNITIES AND NEEDS

**Moderator: Duncan S. MacKenzie**

On February 15, 2001, approximately 30 participants at the First International Tarpon Symposium met after the contributed paper session for a discussion of the current status of tarpon research. During a broad-ranging and constructive discussion of the information presented at the Symposium, the following were identified as future tarpon research needs:

## *Live history studies*

**Adults** Little information is available on the natural history of adult tarpon. In particular, the migratory patterns and distribution of adults in the Gulf of Mexico and Caribbean are poorly understood. Such information will help identify migratory routes and spawning populations, information essential for understanding the origins of animals captured in recreational, scientific, and commercial fisheries. Participants strongly supported a research program to describe the distribution of adult tarpon and to characterize their seasonal movements. In addition to continuation of more traditional tagging programs and fisheries surveys, sophisticated satellite tagging technology, such as pop-up archival tags which can record movements and depths over prolonged periods of time, should be a productive new approach for this wide-ranging species. Scientists and recreational fishermen should be provided with the equipment and training to place tags. Data currently being collected from several sources (e.g., NMFS, Florida League of Anglers, Fish Trackers, Inc., TPWD) should be collected in a centralized database which would serve as a resource for broad scale evaluation of tarpon distribution over time. These studies should be among the highest priorities.

**Juveniles** Identification of juvenile habitat is necessary if nursery areas are to be protected. Channel nets have been a productive and relatively inexpensive method used in Florida for evaluating juvenile tarpon recruitment into nursery areas. A useful expansion of this technology would be to areas where potentially productive tarpon nurseries have yet to be described, such as the eastern coast of Mexico, rather than areas where the density of juveniles appears low (e.g., Central Texas, Louisiana, Costa Rica). Channel net sampling should be used to identify active nurseries, as well as to describe the size, condition, and seasonality of recruits. Channel net sampling should also be progressively expanded into areas of uncertain significance as juvenile habitat (e.g., South Texas) to determine the distribution of tarpon nurseries in the Gulf. Productive

nurseries should be subjected to long-term evaluation to characterize natural fluctuations in juvenile recruitment and help identify the environmental constraints on juvenile density.

**Eggs and Larvae** Whereas the collection of leptocephalus larvae would be useful in identifying spawning habitat and in determining the source of larvae recruited into estuaries, a concerted effort to characterize the reproductive biology of wild tarpon populations (e.g., identification of spawning grounds, observation of spawning activity, collection of fertilized eggs) is probably not economically feasible. It was suggested instead that any survey information currently available on spawning (e.g., from NMFS or state fisheries departments) should be collated to help identify trends in spawning location and timing. It was further suggested that existing NMFS (and any other that can be identified) plankton collections be examined for larval tarpon. Although the group felt that growth studies of larvae would provide valuable information on their migratory capabilities and nutritive requirements, the practical limitations of collecting early life stages in the wild limits the feasibility of these studies, which may be more effectively conducted in the lab (see below).

**New habitats** The interesting suggestion was made that information on environmental requirements and distribution of juvenile and adult tarpon could be obtained from the developing population at the Pacific entrance to the Panama Canal. As this population expands into new habitats, efforts should be made to describe distribution and survival of recruited juveniles using channel net sampling. Tagging of adults in this population would also assist in identifying migratory patterns and environmental requirements of spawning populations.

### *Population genetics*

Interesting molecular genetic data was presented at the meeting. However, it was felt that the diversity of methods for genetic analysis complicated interpretation of the data. It was agreed that standardization of genetic techniques was desirable, as was general access to stored tissue samples for genetic analysis. Microsatellite markers and mitochondrial DNA sequences useful for evaluation of genetic structure of populations should be developed. Primers and probes should be freely available for distribution to all tarpon researchers from a centralized location, providing the opportunity to standardize and replicate molecular genetic techniques. Additionally, a central repository of tissue and scales collected from wild tarpon should be established, guaranteeing all tarpon genetics researchers equal access. Continuing collection of tissues, in the form of scales preserved in alcohol, is clearly needed from as many locations and sources as possible. Once again, recruitment of recreational fishermen into this effort will greatly contribute to its success. Continuation of molecular genetic analysis of populations, coupled with

the better understanding of distribution of adult coming from 1a. above, should also be among the highest priorities.

### *Fisheries studies*

More data is needed on the state of the tarpon fishery in the Gulf and the Caribbean. Information on the numbers and distribution of animals taken by the recreational fishery, as well as the mortality associated with capture, will be very helpful in describing natural populations. Numbers of animals captured and kept by fishermen should be documented and, when possible, descriptive data on fish size and condition obtained. Larger animals captured by recreational fishing techniques should be tagged and followed to determine the impact of catch and release on survival and behavior.

### *Laboratory studies*

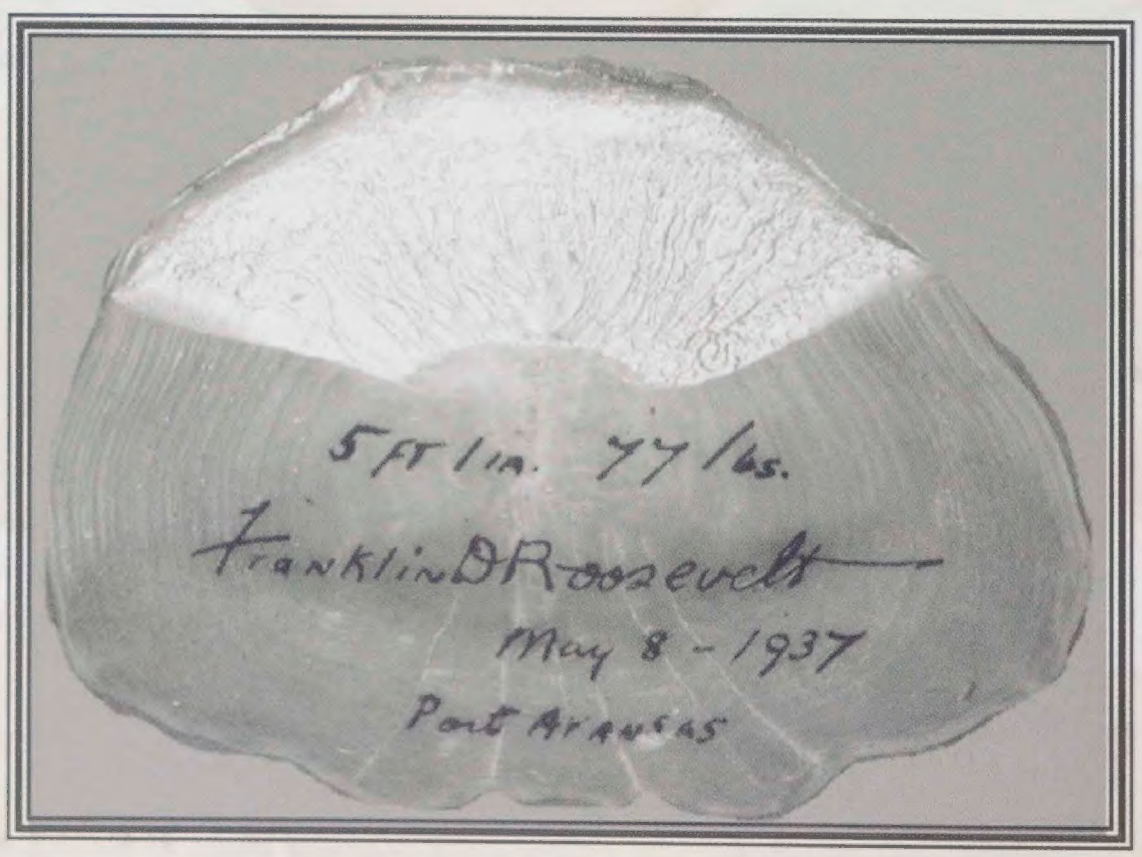
**Microchemistry** Techniques should be developed to provide more detailed and accurate analysis of the growth and migratory activities of wild animals. In particular, otolith microchemistry analysis could be applied to identification of nursery areas and description of migratory patterns. Tissues should be obtained from animals collected in known nurseries and taken by recreational fishermen to develop and validate microchemistry analysis. Otolith microchemistry should be more broadly applied to animals captured in the wild.

**Captive Spawning** Because of the difficulty in obtaining fertilized eggs and larvae in the wild, it was agreed that studies of induced spawning in captive tarpon would be a useful means to provide fertilized eggs and larvae for studies of growth and development dynamics, environmental requirements, and basic physiology. Captive spawning studies could also be used to identify environmental controls of reproductive development and spawning behavior, helpful for understanding the reproductive timing of natural populations. Of particular interest would be the culture of leptocephalus larvae, a potentially challenging endeavor which may nonetheless provide much needed data on the nutritional and habitat preferences of this critical life stage.

**Physiological ecology** Both captive-spawned and wild-collected juveniles should be used for the evaluation of the effects of environmental parameters, such as temperature, on the behavioral and physiological performance of juvenile tarpon. Such studies will be useful in identifying the environmental conditions under which juvenile growth and survival is maximized, and may be particularly useful in evaluating the salinity and temperature tolerance of juveniles in estuarine habitats. Small overwintering juveniles could be obtained from Florida populations for physiological tolerance studies.

### *International collaboration*

Because of the broad ranging migratory behavior of tarpon, international collaboration is essential among researchers from countries bordering the Gulf of Mexico and the Caribbean. Strong support was given for the development of funding specifically earmarked for international interdisciplinary projects on the distribution, life history, and structure of wild tarpon populations. Additionally, resources should be developed to disseminate techniques (e.g., tagging equipment, netting technology, PCR primers) and information (e.g., e-mail lists, listservs) to as many researchers as possible. The International Tarpon Symposium should be held annually, at a rotating location in nations bordering the Gulf of Mexico and Caribbean. Travel funds should be endowed to assure robust international participation at the conference. Efforts should be undertaken to organize a steering committee with the specific charge of increasing the visibility of tarpon concerns among fishermen, regulatory agencies, and funding agencies. Finally, a strong tarpon scientific advisory board should be convened to direct and evaluate future research and funding priorities. These international activities should be among the highest priorities for future research efforts.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